

REVISION OF THE *MYIARCHUS*
FLYCATCHERS OF SOUTH AMERICA

WESLEY E. LANYON

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ABSTRACT

I have spent more than 10 years in the field and in museum study in revising the South American species of the genus *Myiarchus*, the largest genus in the avian family Tyrannidae and one that has given systematists great difficulty.

Specific limits and distributions are defined. An analysis of geographical variation provides a consistent basis for the recognition of subspecies. Four monotypic species (*venezuelensis*, *apicalis*, *semirufus*, and *magnirostris*) and seven polytypic species (*tuberculifer*, *swainsoni*, *phaeocephalus*, *cephalotes*, *panamensis*, *ferox*, and *tyrannulus*), with 20 subspecies, are admitted. No new forms are described.

Diagnoses and keys are based on morphological and vocal characters. Data on vocal repertoires, breeding, and the timing of the annual cycle are

summarized for each species. Special attention is given to documenting cavity-nesting behavior and the nature of the nest lining, as these behavior patterns help to diagnose the genus. Standardized playback of sound recordings and the resulting responses of territorial birds are used to assess the biological significance of differences in vocal characters, particularly in critical studies of allopatric populations. The sequence followed in the presentation of species accounts represents relationships suggested by an analysis of vocal and morphological characters, but the identification of primitive and derived character states must await a comprehensive examination of other genera of tyrannids presumed to be the closest relatives of *Myiarchus*.

RESUMEN

Trabajo de campo y en el museo por un período de más de 10 años, son las bases para esta revisión de las especies sudamericanas del género *Myiarchus*, el mayor y uno de los géneros más difíciles de la familia de aves, Tyrannidae. Límites específicos y áreas de distribución son definidos. Un análisis de variación geográfica provee una base consistente para el reconocimiento de subspecies. Cuatro especies monotípicas (*venezuelensis*, *apicalis*, *semirufus* y *magnirostris*) y siete especies polítípicas (*tuberculifer*, *swainsoni*, *phaeocephalus*, *cephalotes*, *panamensis*, *ferox*, y *tyrannulus*), con 20 subspecies, son reconocidas. No se describen nuevas formas. Diagnoses y claves son basadas sobre caracteres morfológicos y vocales. Datos sobre repertorios vocales, nidificación, y el ciclo anual son resumidos para cada una de las especies. Se presta atención

especial a la documentación de la nidificación en cavidades y el tipo de material con que se tapizan los nidos, puesto que estas normas de comportamiento contribuyen para la diferenciación de los géneros. "Playback" estandarizado de grabaciones de cantos y las respuestas resultantes de aves territoriales, son utilizados para determinar el significado biológico de las diferencias en caracteres vocales, particularmente en estudios críticos de poblaciones alopátricas. El orden seguido en la presentación de las especies representa su parentesco, sugerido por un análisis de caracteres vocales y morfológicos, pero la identificación de caracteres primitivos y derivados tendrán que esperar un examen comprensivo de otros géneros de tiránidos que presumiblemente son los más estrechamente relacionados con *Myiarchus*.

INTRODUCTION

Myiarchus, with 22 species [*vide* Lanyon, in Morony, Bock and Farrand (1957)], is the largest among the 100 or more genera in the family Tyrannidae, one of the three or four largest families of birds. Most avian systematists have admitted difficulty with the discrimination and identification of the various forms within the genus because the specific limits have been equivocal. A remarkable uniformity of plumage coloration and pattern, a lack of

appreciable sexual dimorphism, interspecific overlap in most mensural characters, a misunderstanding with respect to geographical variation, and inadequate or unreliable diagnostic characters have led many museum-based workers to despair that a reasonably satisfactory classification of the group would ever be achieved.

In 1956 I began a series of field and museum studies as a basis for a complete revision

of the genus. Initially I concentrated on the populations of the southwestern United States, Mexico, and Central America (Lanyon, 1960, 1961, 1963b, 1965a, 1965b), and later the West Indies (Lanyon, 1967). Attention was then turned to South American forms, with the first fieldwork being done in Argentina in 1967, followed by 10 subsequent trips to South America through 1976. Other than a brief report on one endemic Peruvian species (Lanyon, 1975a) and the evidence for an incomplete prealternate molt in these forms (Lanyon, 1975b), I have not heretofore published any of the results of my South American research.

The genus presented a challenge to me from the outset. I also realized that if we were to make any progress in understanding relationships among the many forms, a new approach was needed. From field observations and experiments I saw that differences in species-specific vocalizations function as the primary basis for species discrimination among these flycatchers (Lanyon, 1963a), and I became convinced that the use of vocal characters, in conjunction with more conventional morphological characters, would be the key to any successful attempt to determine specific limits and relationships within the genus (Lanyon, 1969). This is the rationale and justification for the descriptive detail on vocal characters I include here.

The present report (1) defines the limits of the South American species of *Myiarchus* and provides diagnoses and keys for their identification; (2) documents the known geographical and ecological distribution of these species; (3) analyzes geographical variation and provides a consistent basis for the recognition of subspecies where appropriate, and (4) summarizes data on breeding and the annual cycle. The sequence I have followed in the species accounts represents relationships among these species suggested by my analysis of their vocal repertoires. Table 1 identifies the basic vocal characters and combinations of these characters in the repertoires of the 11 South American species of *Myiarchus* delimited in this study. This clustering of species according to shared complexes of vocal characters is supported by external morphological characters. For example, the three species at the right of the table

(*semirufus*, *tyrannulus*, and *magnirostris*) are the only South American members of the genus that, in adults, have the rectrices conspicuously marked with Antique Brown and have the mouth-lining (freshly collected specimens) pale Orange-Yellow rather than nearer Spectrum Orange as in all of the remaining species (see Smithe, 1975 for capitalized color names). The cluster of species in the middle of the sequence (*apicalis* through *panamensis*) are those that have varying amounts of white on the outer rectrices. The polarity of these assemblages of species and the identity of shared and derived character complexes must await a comprehensive examination of other genera of tyrannids presumed to be the closest relatives of *Myiarchus*.

The inclusion of the Galapagos form of *Myiarchus* ("Eribates") in this report on South American species is a matter of expediency, as all remaining West Indian and Middle American forms have been treated elsewhere, but nevertheless indicates my conviction that it truly belongs in this genus. On the other hand, *Nesotriccus* (Cocos Island) has been omitted for I do not believe it to be congeneric with *Myiarchus*. Fieldwork in this study had to be extended into southern Middle America to include the complete ranges of *M. tuberculifer brunneiceps* and *M. p. panamensis*, both of which occur in Panama, and to acquire experience with *M. panamensis actiosus*, the northernmost population of the species. One North American species, *M. crinitus*, is present in Colombia and Venezuela during the winter months (October to May) but is considered extralimital here.

The previous revisions of the South American species of *Myiarchus* are summarized in table 2, and are compared with the classification that I propose in the present report. Detailed discussions of these taxonomic treatments are included in the various species accounts, where appropriate.

ACKNOWLEDGMENTS

I am deeply grateful to the superb field assistants who traveled with me and shared the tasks of reconnaissance for territorial birds, tape recording of vocal characters, conducting

standardized playback experiments, and collecting specimens of known voice. None will soon forget those long days of hiking and carrying recording and collecting gear for seemingly interminable miles. David Ewert assisted me on four of the 11 trips to South America. My wife, Vicky, and my son, Scott, participated on three and two of the trips, respectively. George Powell, Curtis Adkisson, and Thomas Jacikoff each accompanied me on a single trip.

Fieldwork was greatly facilitated by, and in

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TABLE 1
Distribution of Vocal Characters Among South American Species of *Myiarchus*

	<i>tuberculifer</i>	<i>venezuelensis</i>	<i>swainsoni</i>	<i>apicalis</i>	<i>phaeocephalus</i>	<i>cephalotes</i>	<i>panamensis</i>	<i>ferox</i>	<i>semirufus</i>	<i>tyrannulus</i>	<i>magnirostris</i>
"wheeler-r-r" note	X	X	—	—	—	—	—	—	—	—	—
rasp-roll	X	—	X	—	—	—	—	—	—	—	—
dawn song whistles											
isolated, plaintive	X	X	X	?	—	—	—	—	—	—	—
rolls=train of											
pulsed "huits"	X	—	X	X	/	—	—	—	—	—	—
dawn song whistles											
sharp or in series	—	—	—	?	X	X	—	—	—	—	—
rasp-whistle	/	X	/	—	—	X	—	—	—	—	—
rolls=train of											
sharp whistles	—	—	Xs	—	—	/	X	—	—	—	—
series of virtually											
unmodulated whistles	—	—	—	X	X	X	—	/	X	—	—
hiccup note	X	X	Xs	X	X	Xs	X	X	X	—	—
rasp (modulating											
frequency > 70 Hz.)	X	X	X	—	—	X	—	—	/	X	X
"huit" note	/	—	X	X	—	—	/	/	X	X	X
rasping whistle	—	—	/	—	X	/	X	X	X	—	—
dawn song=only											
vibrato notes	—	—	—	—	—	—	X	X	—	—	—
vibrato whistles in											
daytime repertoire	—	—	—	—	—	/	X	X	—	X	X
rattle note	—	—	—	—	—	—	—	X	—	—	—
dawn song has "huits"											
and rasping whistles	—	—	—	—	—	—	—	—	X	—	—
rapid "huits"	—	—	—	—	—	—	—	—	—	X	X
"whay-burg" notes	—	—	—	—	—	—	—	—	—	X	X
dawn song has "huits"											
but no rasping or											
plaintive whistles	—	—	—	—	—	—	—	—	—	X	X

X, Prominent in repertoire; /, recorded, but not regularly; s, some populations only; ?, dawn song unknown; —, absent in repertoire.

TABLE 2
Previous and Proposed Taxonomy of the South American Species of *Myiarchus*

Todd (1922)	Hellmayr (1927)	Zimmer (1938a; MS) ^a	Proposed
<i>M. tuberculifer</i>	<i>M. tuberculifer</i>	<i>M. tuberculifer</i>	<i>M. tuberculifer</i>
<i>M. t. tuberculifer</i>	<i>M. t. tuberculifer</i>	<i>M. t. tuberculifer</i>	<i>M. t. tuberculifer</i>
		<i>M. t. clarus</i>	(synonymized with <i>tuberculifer</i>)
<i>M. t. tricolor</i>	<i>M. t. tricolor</i>	<i>M. t. tricolor</i>	(synonymized with <i>tuberculifer</i>)
(not described)	(not described)	<i>M. t. pallidus</i>	<i>M. t. pallidus</i>
(extralimital)	<i>M. t. brunneiceps</i>	<i>M. t. brunneiceps</i>	<i>M. t. brunneiceps</i>
<i>M. t. nigriceps</i>	<i>M. t. nigriceps</i>	<i>M. t. nigriceps</i>	<i>M. t. nigriceps</i>
<i>M. atriceps</i>	<i>M. t. atriceps</i>	<i>M. t. atriceps</i>	<i>M. t. atriceps</i>
<i>M. ferox venezuelensis</i>	<i>M. ferox venezuelensis</i>	<i>M. ferox venezuelensis</i>	<i>M. venezuelensis</i>
(synonymized with <i>ferox</i>)	<i>M. ferox insulicola</i>	<i>M. ferox insulicola</i>	(synonymized with <i>venezuelensis</i>)
	<i>M. swainsoni</i>	<i>M. swainsoni</i>	<i>M. swainsoni</i>
<i>M. sordidus</i>	(synonymized with <i>swainsoni</i>)	<i>M. s. swainsoni</i>	<i>M. s. swainsoni</i>
		(synonymized with <i>swainsoni</i>)	(synonymized with <i>swainsoni</i>)
<i>M. pelzelni</i>	<i>M. pelzelni</i>		
<i>M. pelzelni</i>	<i>M. p. pelzelni</i>	<i>M. s. pelzelni</i>	<i>M. s. pelzelni</i>
(synonymized with <i>pelzelni</i>)	<i>M. p. ferocior</i>	<i>M. s. ferocior</i>	<i>M. s. ferocior</i>
<i>M. phaeonotus</i>	<i>M. phaeonotus</i>	<i>M. s. phaeonotus</i>	<i>M. s. phaeonotus</i>
(not described)	(not described)	<i>M. s. amazonus</i>	(intergrades between <i>pelzelni</i> and <i>phaeonotus</i>)
<i>M. apicalis</i>	<i>M. apicalis</i>	<i>M. apicalis</i>	<i>M. apicalis</i>
<i>M. phaeocephalus</i>	<i>M. phaeocephalus</i>	<i>M. phaeocephalus</i>	<i>M. phaeocephalus</i>
		<i>M. p. phaeocephalus</i>	<i>M. p. phaeocephalus</i>
(not described)	(not described)	<i>M. p. interior</i>	<i>M. p. interior</i>
(not described)	<i>M. toddi</i>	<i>M. p. toddi</i>	(aberrant specimen of <i>phaeocephalus</i>)
<i>M. cephalotes</i>	<i>M. cephalotes</i>	<i>M. cephalotes</i>	<i>M. cephalotes</i>
	<i>M. c. cephalotes</i>	<i>M. c. cephalotes</i>	<i>M. c. cephalotes</i>
(not described)	(not described)	<i>M. c. cauae</i>	(synonymized with <i>cephalotes</i>)
(not described)	(not described)	<i>M. c. gularis</i>	(synonymized with <i>cephalotes</i>)
(not described)	<i>M. c. caribbaeus</i>	<i>M. c. caribbaeus</i>	<i>M. c. caribbaeus</i>
<i>M. ferox panamensis</i>	<i>M. ferox panamensis</i>	<i>M. ferox panamensis</i>	<i>M. panamensis</i>
(not described)	(not described)	<i>M. ferox audens</i>	<i>M. p. panamensis</i>
			(synonymized with <i>panamensis</i>)
(extralimital)	<i>M. ferox actiosus</i>	<i>M. ferox actiosus</i>	<i>M. p. actiosus</i>
<i>M. ferox</i> ^b	<i>M. ferox</i> ^c	<i>M. ferox</i> ^d	<i>M. ferox</i>
<i>M. f. ferox</i>	<i>M. f. ferox</i>	<i>M. f. ferox</i>	<i>M. f. ferox</i>
(not described)	<i>M. f. subsp.</i>	<i>M. f. brunnescens</i>	<i>M. f. brunnescens</i>
<i>M. F. "swainsoni" = australis</i>	<i>M. f. australis</i>	<i>M. f. australis</i>	<i>M. f. australis</i>
<i>M. semirufus</i>	<i>M. semirufus</i>	<i>M. semirufus</i>	<i>M. semirufus</i>
<i>M. tyrannulus</i>	<i>M. tyrannulus</i>	<i>M. tyrannulus</i>	<i>M. tyrannulus</i>

TABLE 2 — (Continued)

Todd (1922)	Hellmayr (1927)	Zimmer (1938a; MS) ^a	Proposed
<i>M. t. tyrannulus</i> (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>) (not described)	<i>M. t. tyrannulus</i> <i>M. t. chlorepsciscus</i> <i>M. t. tobagensis</i> <i>M. t. brevipennis</i> (not described)	<i>M. t. tyrannulus</i> (synonymized with <i>tyrannulus</i>) <i>M. t. tobagensis</i> <i>M. t. brevipennis</i> <i>M. t. blaquillae</i>	<i>M. t. tyrannulus</i> (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>) (synonymized with <i>tyrannulus</i>)
<i>M. t. bahiae</i> <i>M. t. pallescens</i> (extralimital)	<i>M. t. bahiae</i> <i>M. t. pallescens</i> <i>Eribates magnirostris</i>	<i>M. t. bahiae</i> (synonymized with <i>bahiae</i>) <i>M. magnirostris</i>	<i>M. t. bahiae</i> (synonymized with <i>bahiae</i>) <i>M. magnirostris</i>

^aMeyer de Schauensee (1966) followed Zimmer's treatment of species.

^bTodd also included *venezuelensis* and *panamensis* in *M. ferox*, as listed earlier in this column.

^cHellmayr also included *venezuelensis*, *insulicola*, *panamensis*, and *actiosus* in *M. ferox*, as listed earlier in this column.

^dZimmer also included *venezuelensis*, *insulicola*, *panamensis*, *audens*, and *actiosus* in *M. ferox*, as listed earlier in this column.

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could be made available for this study. Mary LeCroy and Robert Koestler assisted with the spectrophotometric analyses of plumage reflectance.

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ABBREVIATIONS

A total of 4590 specimens was examined during this study, including 325 that I collected. Abbreviations in the following list of museum and private collections are used in the text, often in association with catalogue numbers:

- AMNH, The American Museum of Natural History, New York
 ANSP, the Academy of Natural Sciences, Philadelphia (Frank B. Gill)
 BM, British Museum (Natural History), Tring (David Snow)
 CM, Carnegie Museum, Pittsburgh (Kenneth C. Parkes)
 FMNH, Field Museum of Natural History, Chicago (Melvin A. Traylor, Jr.)
 ICN, Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (Hernando Romero)
 IML, Instituto "Miguel Lillo", Tucumán (Claes Olog)
 LAM, Los Angeles County Museum, Los Angeles (Kenneth E. Stager)
 LSU, Louisiana State University Museum of Zoology, Baton Rouge (George H. Lowery, Jr.)
 MACN, Museo Argentino de Ciencias Naturales, Buenos Aires (Jorge R. Navas)
 MC, Moore Collection, Occidental College, Los Angeles (John W. Hardy)
 MCZ, Museum of Comparative Zoology, Harvard University (Raymond A. Paynter, Jr.)
 MHNL, Museo Historia Natural "Javier Prado," Lima (Hernando Macedo)
 MLP, Museo de La Plata, La Plata (Nellie Bo)
 MNHL, Museum of Natural History, Leiden (G. F. Mees)
 MNHM, Museo Nacional de Historia Natural, Montevideo (Juan Cuello)
 MNRJ, Museu Nacional, Rio de Janeiro (Helmut Sick)
 MVZ, Museum of Vertebrate Zoology, University of California, Berkeley (Ned K. Johnson)
 MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo (Helio Camargo)
 PC, Colección Ornitológica Phelps, Caracas (William H. Phelps, Jr.)
 PMNH, Peabody Museum of Natural History, Yale University, New Haven (Charles G. Sibley)
 RGC, Colección Ornitológica, Estación Biológica de Rancho Grande, Maracay, Venezuela (Paul Schwartz)
 SC, Collection of A. Schwartz, Miami, Florida

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (George E. Watson)

MUSEUM WORK

Linear measurements were taken in millimeters: wing length, flattened; tail length, from the insertion of the central rectrices, with calipers; bill length, from the anterior margin of the nostril. The ratio of tail length to wing length is expressed in percent. In the two wing formulae used to measure differences in wing shape, the primaries are numbered from the inner part of the wing outward, with the outermost primary being number 10. The wing is held in its normal, closed position alongside the body, without any distortion of the primaries. In the formula "fifth primary minus ninth primary," the difference between the lengths of these two primaries is determined by the distance from the tip of the shorter primary to the tip of the longer primary. Care must be taken to observe the mathematical sign in such measurements; the difference will be + when the fifth primary is the longer, and - when the fifth primary is the shorter of the two. Likewise, in the formula "fourth primary minus tenth primary," the difference will be + when the fourth primary is the longer, and - when the fourth primary is the shorter of the two.

Capitalized names of color, as in plumage descriptions in the diagnoses, refer to specific colors depicted in Smithe (1975).

Simplified but standardized terms have been used in the keys and diagnoses to indicate degree of statistical reliability. My phrase "nearly always" is roughly equivalent to the statistical statement that "98 out of 100 individuals may be expected to be so characterized," and, conversely, "rarely" suggests that "only two out of 100 may be so characterized." My term "usually," in the keys and diagnoses, is equivalent to the statement that "90 out of 100 individuals may be so characterized," based on the material analyzed. The statistical data to support such statements are given in the tables of measurements to be found in each of the species accounts.

FIELDWORK

I made eleven trips to South America over the 10-year period 1967 to 1976, for a total of 14 months of fieldwork. The inclusive dates of these trips and the countries visited are as follows:

1. October 21 to December 22, 1967; Argentina, Uruguay, and Brazil
2. April 21 to May 31, 1968; Curaçao, Venezuela, and Tobago
3. April 16 to May 26, 1969; Panama and Venezuela
4. April 27 to May 28, 1970; Venezuela and Colombia
5. November 5 to December 23, 1970; Argentina, Brazil, and Surinam
6. October 29 to November 25, 1972; Peru
7. February 21 to April 2, 1973; Peru and Colombia
8. December 17, 1973, to January 14, 1974; Peru and Ecuador
9. April 14 to May 12, 1974; Colombia and Venezuela
10. October 12 to November 23, 1974; Bolivia
11. January 25 to March 10, 1976; Colombia, Ecuador, Galapagos, and Costa Rica

A detailed itinerary is presented within each species account.

At each locality our procedure was to (1) locate as many territorial pairs of *Myiarchus* as possible (using reconnaissance tapes of the vocal characters of the expected species, when available); (2) obtain sound recordings of the vocal characters of these territorial birds; (3) observe breeding behavior and document nest sites whenever possible; (4) photograph habitat; (5) conduct standardized playback experiments to test the ability of territorial birds to discriminate between their own vocal characters and those of other forms; (6) collect specimens whose vocal characters had been recorded on tape, and (7) photograph the color of the mouth lining in fresh specimens.

Closeups of the mouth lining color in fresh specimens were taken with a Kodak Startech Camera equipped with a 1:1 accessory lens system, Ektachrome-X film, an 82A filter, and

M3B flashbulbs. Habitat photographs were taken with Kodachrome II or 64 film, often with a 35 mm. lens. A 300 mm. lens was used for some scenes of adult birds at nests. All photographs reproduced are by the author unless otherwise stated. A Pesola scale was used to determine body weight, in grams, of freshly collected specimens. A total of 325 specimens of *Myiarchus* was collected on these trips, and nearly all of these had their vocal characters recorded on tape before they were collected. It was this nucleus of specimens of known voice that was used as a basis for a more enlightened examination of the large number of South American *Myiarchus* already extant in museum collections.

STANDARDIZED PLAYBACK EXPERIMENTS

I have advocated (Lanyon, 1967, 1969) the use of standardized playback of sound recordings and the responses of territorial birds so as to assess the biological significance of differences in vocal characters between populations. Experiments with such playback are especially informative and critical in analyses of allopatric populations. It is mainly in such circumstances that I have used this technique in the present study. Territorial birds can discriminate between their own vocal characters and those of other populations, as well as of other species, when sound recordings are played back simultaneously to simulate a condition of "sympatry." This is in many cases the best index of reproductive isolation available for allopatric forms.

I had from previous field studies standardized playback tapes for all the West Indian and North and Middle American species of *Myiarchus*. New tapes were prepared for the South American forms, using representative recordings of the vocal characters of each form with respect to its response to intruding conspecifics and its dawn song. Each experiment consisted of dual sets of auditory and visual stimuli provided simultaneously. The standardized tapes were played back on two Uher tape recorders without additional amplification (fig. 1). Speaker cables permitted operation of the re-

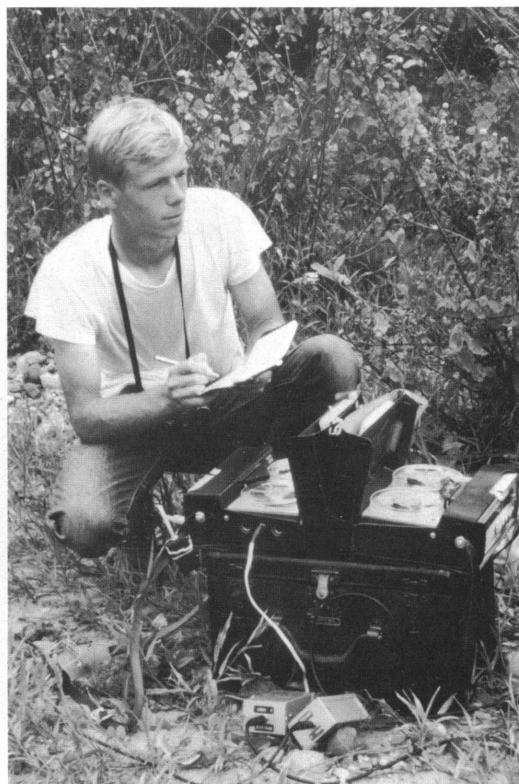


FIG. 1. *Left:* Author with Uher tape recorder and parabolic reflector, recording vocal characters of *Myiarchus semirufus* near Casma, Peru, December 1973. *Right:* David Ewert, field assistant, notes ability of territorial *Myiarchus ferox brunnescens* to discriminate between two standardized *Myiarchus* recordings played back simultaneously on two Uher recorders. Cables permit remote operation of two speakers. Táchira, Venezuela, May 1969.

corders at 50-foot distances from two Electrovoice speakers set approximately 100 feet apart. Two identical plastic models of the approximate size and color of a *Myiarchus* flycatcher were positioned above the speakers for visual stimuli. No effort was made to vary the visual stimuli in these experiments, for previous experience with the North and Middle American species of *Myiarchus* revealed that territorial birds exhibit hardly any visual discrimination (Lanyon, 1963). The plastic models served to provide focal points for the responses of the territorial birds to the auditory stimuli emanating from the speakers below. Most experiments consisted of 14 minutes of playback of any two of my standardized playback tapes.

After the first seven minutes of playback, the cables of the two speakers were interchanged, so that during the remaining seven minutes the positional sources of the two sets of auditory stimuli were reversed. Each experiment thus provided two opportunities to observe orientation by territorial birds to one or the other of the two sets of auditory stimuli: an initial orientation at the start of playback, and a second or reorientation following the interchange of cables. Notes were taken of the responses of the territorial birds, particularly with respect to their orientation or changes in orientation to one or both sets of speakers and models. A bird was considered to have given a positive response to a particular repertoire if it oriented

to within 30 feet of the plastic model and remained within that distance for all or nearly all of the seven-minute period during which the repertoire emanated from the speaker associated with that model. For each positive response there was recorded a corresponding negative response to the other repertoire, which was emanating from the second speaker. Each positive response could be classified further according to its intensity, i.e., whether the bird actively engaged in short flights in the vicinity of the model ("crisscrossing"), or flew toward the model itself ("pass"), or perched within a few feet of the model ("study"), or actually made contact with the model ("attack"). Excerpts from notes taken during these playback experiments are used in many of the species accounts to provide experimental evidence in support of positions taken on the taxonomic relationships of pairs of species or subspecies.

ANALYSIS OF VOCAL CHARACTERS

Sound recordings were made with a Uher 4000 Report L tape recorder, operated at a tape speed of 19 cm. per second, and either a Uher M517 microphone or an Altec 660B microphone mounted at the focal point of a 61 cm. fiberglass parabolic reflector (fig. 1). A Uher microphone gain amplifier, 106GA, was generally used to provide additional signal amplification. Whenever a new recording was made in the field, the tone of a pitch pipe (middle "A," 440 Hz.) was recorded as a permanent and convenient check on the speed of the recorder at that instant and a check for possible distortion. Such careful documentation of tape speed is critical in analyses of intraspecific variation in the frequencies of vocal characters. I estimate that I have about 36 hours of recordings of South American *Myiarchus*, on nearly 25 km. (15 miles) of recording tape. Sample sizes have been indicated in the sections dealing with the vocal characters of the various species.

Representative vocal characters were selected for analysis with a Sona-Graph, model 6061B. Both narrow-band (45 Hz.) and wide-band (300 Hz.) filters were used, for increased resolution in frequency and time, respectively, and the displays illustrated here have been

identified accordingly. Thousands of sound spectrograms were studied as the basis for the descriptions of the vocal characters of the various species, and for an analysis of geographical variation within each species. To illustrate the extent of intraspecific variation in vocal characters, sound spectrograms representing ranges of variation were then photographed and are reproduced here as halftone illustrations, thus retaining the maximum detail possible. The sound spectrograms graphically portray frequency (kHz. = kiloHertz = kilocycles per second) against time (seconds). Locality and other data for the sound recordings used in the spectrograms reproduced here are given in the Appendix.

The *carrier frequency*, or rate of oscillation, is that sound energy produced by an oscillator (in the syrinx) vibrating at its natural frequency (pitch). Variation in the carrier frequency is produced by tension applied to the oscillator, in this case by syringeal muscles acting upon the internal tympaniform membrane. The carrier frequency may also vary in *amplitude* (intensity or loudness).

Modulation is the modification of the sound energy in frequency, amplitude, or both. A steady-state condition produces an unmodulated carrier frequency. It is the nature of this modulation that determines the quality of the sound. The spectrographic display of a modulated carrier frequency varies according to the *modulating frequency*. The very simplest type of modulation is a whistled note that is only gradually slurred from one frequency to another, resulting in a *glissando*. As the modulating frequency increases, the display becomes more "wavelike" in appearance, as, for example, in the slightly tremulous effect of a *vibrato*. When the modulating frequency is too rapid for an accurate portrayal by the Sona-Graph (above 70 Hz.), the narrow-band filter displays the modulated signal as a carrier frequency and side-band frequencies (spaced at intervals equal to the modulating frequency). When the wide-band filter is used, the modulating frequency is revealed by the frequency (or spacing) of the vertical streaks. Such displays tell us little as to whether it is the amplitude or frequency or both that is being modulated.

Deviation from the carrier frequency is the vertical spread of the trace about the central frequency, and is determined by the amplitudes of the carrier frequency and the modulating frequency relative to one another. A carrier frequency may vary in its *frequency excursion*, i.e., the range of frequencies represented throughout the duration of a particular vocalization. A whistled note may have little or no frequency excursion and consequently sound plaintive to the human ear, or it may range over one or more kiloHertz within a brief period of time and thus have a very sharp, piercing quality. Because of the ease with which the circuitry of the Sona-Graph can be overloaded, spurious harmonics are common in sound spectrograms and difficult if not impossible to differentiate from true harmonic spectra that are produced by some birds. For this reason, harmonics have purposely been eliminated from most of the sound spectrograms illustrated here.

Birds are believed to have the potential for the production of sound from two sound generators, that is, from both bronchi in the syrinx. Normally, perhaps, the two sources produce signals in concert. Now there is sufficient evidence to show that some species can produce two simultaneous signals that are independent of each other and harmonically unrelated. In South American *Myiarchus* most vocal characters show no evidence of this phenomenon. In the two species where it does occur this has been noted.

When there is a "gating" effect upon the carrier frequency that results in a rapid sequence or train of discrete but virtually identical (with respect to the spectrographic display) bursts of energy, I refer to this as pulsation, the carrier frequency being *pulsed* in this instance.

For more detailed presentations of the acoustics and probable physiology of avian vocalizations, and of the use of the Sona-Graph for the analysis of these sounds, see Greenewalt (1968), Stein (1968), and Davis (1964).

The vocal characters of *Myiarchus* can be categorized conveniently as either *calls* or *dawn song*, as defined below.

CALLS: Both sexes share the same repertoire of calls given during the daylight hours. These calls are ritualized sound signals used to com-

municate such information as location, specific identity, territorial limits, alarm, and other reproductive and social functions. Special attention has been given in the sections on vocal characters to those calls that characterize the vocal response of a species to the playback of a recording of its own vocal repertoire or in natural encounters with intruding conspecifics.

Most South American *Myiarchus* have five or six basic types of calls in their repertoire. The differences between calls, to the human ear, may be due to differences in frequency, duration, modulating frequency, frequency excursion, number of syllables, deviation from the carrier frequency, pulsation of the carrier frequency, or evidence for the simultaneous production of two independent signals harmonically unrelated. To identify the variety of calls that make up the repertoire of a *Myiarchus* flycatcher, I have labeled them according to their phonetics, an appropriate simile, or their general quality or pattern. Those basic calls shared by several species are here described in a general way, to avoid unnecessary duplication later.

The carrier frequency in the calls of these flycatchers is restricted to the 1.0 to 5.0 kHz range; generally, however, it ranges from 2.0 to 3.0 kHz. There is an inverse correlation between body size and carrier frequency, with smaller birds having somewhat higher frequencies than their larger-bodied relatives. This has been carefully documented for *M. tuberculifer*, in which there is appreciable geographical variation in body size.

The simplest call, and one shared by most species, is a brief rendition of the carrier frequency that I name the "*huit*" (equivalent to the "whit" of some workers). Apparently it has been secondarily lost in a few species, and there are conspicuous differences in the prominence of this call within the repertoires of the other species. Typically this single syllable is displayed spectrographically as a chevron-like trace (fig. 2:6), though it may appear only as the ascending segment of a chevron (fig. 3:6, 7), particularly under circumstances of intense excitement. There are no useful specific differences in the configuration of the "*huit*," and one must be aware that the frequency excursion

of sound signals of such short duration may be exaggerated in spectrographic display, for the Sona-Graph is unsuited for handling such signals.

If the carrier frequency is pulsed for a second time, immediately following the rendition of the "huit," a two-syllable call results, which I have termed the *hiccup* (fig. 8:10-21). Most species have this call, though it has apparently been lost in certain subspecific populations. Those species that do not have a hiccup, as defined here, have substituted a related call also derived from the basic "huit." There are specific differences in the hiccup, depending upon which syllable is accented (greater amplitude and/or greater frequency excursion) and upon the complexity of the spectrographic display.

A third basic type of call, the *whistle* (fig. 3:1-4), is produced by a sustained rendition of the carrier frequency without modulation (steady-state, "pure tone") or with slight modulation (gradually slurred from one frequency to another; a *glissando*). Most species have some form of whistled note in their repertoires, but there are specific differences in the prominence of the whistles in the repertoire and in their duration and degree of modulation. Prolonged, virtually unmodulated whistles sound plaintive to the human ear, while shorter whistles with prominent glissando (rapid change in frequency) have a sharp, piercing quality (fig. 3:1).

The carrier frequency of these flycatchers can be modulated at a frequency of up to 100 Hz., and there are differences among the species in both the frequency of modulation and the deviation from the carrier frequency. When the modulating frequency is less than about 30 Hz. the spectrographic trace is wavelike and the effect is a slightly tremulous musical note, or *vibrato* (fig. 3:13-16). Somewhat higher modulating frequencies, up to about 60 cycles per second, begin to produce a rasping quality, and I term such calls *rasping whistles* (fig. 2:13-14). The highest modulating frequencies, from 70 to 100 Hz., result in a call I refer to as the *rasp* (fig. 2:7, 8). It sounds noisy and grating to the human ear, and the spectrographic display will feature side-bands above and below the carrier frequency (narrow-band

filter) or a series of vertical streaks along the carrier frequency (wide-band filter). The rasp can be converted into a virtually unmodulated whistle without interruption of the sound signal. The resulting call, the *rasp-whistle* (fig. 2:9, 10), demonstrates the manner in which the carrier frequency can be modified and controlled, in an uninterrupted continuum, to produce the repertoire of calls that characterize each species.

The *roll* is a multi-syllabled call that results from a rapidly delivered series of pulsed renditions of the carrier frequency. There are differences among the species with regard to the configuration of the traces of the individual syllables, for they may be chevron-like (typical "huit" notes; fig. 2:3) or they may be of longer duration, whereby the roll becomes a very rapid train of whistled notes (fig. 2:4). Some species have no roll in their repertoire, while others only use this call sparingly. One species has modified this call by frequently, perhaps invariably, using two sound generators. The result, the *rattle* (fig. 2:15), has a more penetrating and strident quality than does the roll of other species. Again, the variable but precise control of the carrier frequency in these birds is illustrated by the fact that the roll may be introduced by either a rasp or a whistle, as part of a continuum of uninterrupted sound energy, and is sometimes also terminated with a rasp (fig. 2:2).

DAWN SONG: The males of every species of *Myiarchus* give a stereotyped, species-specific pattern of vocalizations just prior to, and at, dawn, beginning at the onset of territorial defense and extending for varying lengths of time through the breeding season. Many genera of tyrannid flycatchers exhibit this vocal behavior, which has become known in the literature as the "dawn song." There are no notes unique to dawn song in *Myiarchus*, i.e., no vocal components that cannot also be heard during the day. In fact, the components of dawn song are often those vocalizations used by both sexes during the day for maintenance of the pair bond. The unique features of dawn song are the arrangements of these components into predictable patterns, often having consistent temporal characteristics, and the repetition of these patterns

in a nearly unbroken sequence for a period of from 15 to 30 minutes at dawn during the breeding season.

In those instances where the components of dawn song consist of only one basic daytime call, such as a whistle, that call may also be heard at any time during the day. Even when dawn song is more complex, consisting of a precise pattern of several of the basic daytime calls, it may be heard at other times of day but much less frequently and predictably (e.g., under reduced levels of light intensity, such as at dusk or under a heavy cloud cover).

ANALYSIS OF PLUMAGE REFLECTANCE

For an objective, quantitative measurement of differences in plumage coloration, in those few instances where such differences were thought to be critical in a determination of relationship, use was made of a Diano/Hardy recording spectrophotometer with automatic computer print-out. This equipment was used to measure the reflectance characteristics of only two regions of the plumage: small, carefully selected areas of the center of the crown and of the center of the back. The reflectance of a beam of light from the sample, a specimen of *Myiarchus*, was compared with the reflectance of the same beam of light from a white standard, in this instance a block of Carrara marble, as a function of wave-length over the range of the visible spectrum. The adjustable iris diaphragm within the spectrophotometer was closed down to reduce the diameter of the effective beam of light to 8 mm. The sizes of the sample and standard ports of the integrating sphere were reduced to 11 mm. in diameter, in order to limit the area of the crown and back that would actually reflect light. A plate of optical glass (Type BK7) was inserted over both sample and standard ports to prevent dust and feather fragments from falling into the sphere. When a specimen was pressed against this glass plate, the feathers were compressed more or less into a single plane, thus insuring that the feathers remained at a constant distance from the light source. All measurements were made with "illuminant C," "lamp dim," and "spectral component excluded," the last in an

attempt to exclude light reflected specularly from the surface of the feathers.

The "absolute" reflectance values for each specimen were converted automatically by the computer into the tristimulus notations (X, Y, and Z) of the International Commission on Illumination, which numerically characterize the plumage color as viewed by a "standard observer" under a "standard condition of illumination" (see discussions in Judd, 1933; Hardy, 1936; Billmeyer and Saltzman, 1966; and Dyck, 1966). The means of these numerical values for all specimens in a given sample were then computed to represent the reflectance characteristics of that sample. The most important of these tristimulus values, with respect to this particular analysis of the rather dull plumage of the crown and back of *Myiarchus*, is Y, which corresponds to the relative luminance, brightness, or intensity of the light reflected from the sample. This value of Y is termed *brightness* in the tables and text here, and is expressed in percent; the lower the percent brightness, the darker the color of the plumage.

In addition to brightness, I had the computer transform the tristimulus values into notations that are better suited for the comparison and discrimination of small color differences such as occur between various forms of *Myiarchus*. The system adopted here was developed by MacAdam (1943) for the calculation and representation of small color differences between a sample and a standard; the formulas for these calculations are available from me upon request. I have utilized two *color difference* outputs from this system in my analysis of the reflectance characteristics of *Myiarchus*, and both of these are expressed in *MacAdam units*. One MacAdam unit of color difference is roughly equivalent to a "just-perceptible difference" in color for the "average human observer." One of these outputs, termed *DL* here, is still another measure of brightness, but differs from percent brightness (as derived from Y) in that the value given for each sample is relative to a particular standard. In each table of reflectance characteristics, a DL value is given for each sample and this value is an index of the degree of color difference between that sample and the standard. A DL value with

a + sign indicates that the sample is brighter than the standard, whereas a sample having a DL value with a - sign is darker than the standard; the larger the value, the brighter the sample relative to the standard. The other out-

put, termed *DE* here, is an approximation of "overall color difference" between the reflectance characteristics of sample and standard, since it is a function of hue and chroma (see Smithe, 1974) as well as brightness.

KEYS TO THE SOUTH AMERICAN SPECIES OF *MYIARCHUS*

EXTERNAL MORPHOLOGY OF ADULTS

Construction of a key to these species that is based solely on morphological characters and that will work reliably for all specimens is impossible without including so many qualifying remarks and exceptions as to make the key unworkable. Seasonal differences due to feather wear, geographical variation within wide-ranging and polytypic species, and changes in bill color in museum specimens are some of the problems encountered when one searches for usable characters. I have not attempted to include specimens in juvenal plumage, for the presence of Antique Brown in the rectrices of the juvenals of all species of *Myiarchus* obfuscates the use of this character in diagnosing those species that retain this coloration in the definitive plumage. There is the additional problem that we still do not have adequate series, numerically and geographically, to characterize the juvenal plumages of some species. Since intraspecific variation in plumage coloration and pattern often exceeds the differences that one finds between species, one is tempted to construct a key to identify well-marked forms, rather than species, but then there would be the problem of how to treat specimens from

zones of intergradation between these well-marked subspecies. To avoid this problem I have elected to confine the key to the species level.

After many false starts and after discarding and substituting characters at all levels, I arrived at the following key, which is something of a compromise in terms of number of qualifications and exceptions. It should be adequate for the routine identification of 95 percent or more of the specimens of adult South American *Myiarchus*. The characters used at the beginning of the key are the more obvious, less ambiguous ones, and hence there is a greater degree of probability that all specimens of the first seven species will be keyed out correctly. There is no substitute, however, for the practice of comparing "unknowns" with good museum series, and the identification of critical or unique specimens should be confirmed in that manner. An identification to species resulting from the use of this key should be checked against the diagnosis for that species, to which the reader is referred.

My methods for measuring mensural characters and wing shape, and my simplified terms for estimating statistical reliability are discussed under "Museum Work."

- 1 — Inner vanes of rectrices conspicuously marked (at least 3 mm. wide on one or more rectrices) with Antique Brown¹; mouth lining of freshly collected specimens pale Orange Yellow
- 2 — Plumage of underparts nearly uniformly Cinnamon *M. semirufus* (p. 581)
- 2A— Plumage of underparts some shade of yellow (abdomen) and of gray (throat and chest)
- 3 — Wing length more than 80 mm. and tail length more than 74 mm. *M. tyrannulus* (p. 587)²

¹Ridgway (1907) used "cinnamon-rufous" for this color, and that term has been followed subsequently by most ornithologists. Smithe (1974, p. 109) has pointed out that this color is closer, visually and spectrophotometrically, to Ridgway's (1912) Antique Brown, a color name which Smithe adopted.

²Wintering specimens of *M. crinitus* (from North America) will also key out here, but have more Antique Brown in the

- 3A— Wing length less than 80 mm. and tail length less than 74 mm. *M. magnirostris* (p. 603)
- 1A— Inner vanes of rectrices not conspicuously marked as above; mouth lining of freshly collected specimens nearer Spectrum Orange
- 4 — Rectrices with conspicuous and extensive whitish tips; pale tip of outer rectrix extends at least 8 mm. along the rachis *M. apicalis* (p. 534)
- 4A— Not as in 4 above
- 5 — Outer vanes of outer pair of rectrices noticeably paler than inner vanes, and external margins of inner rectrices *conspicuously* fringed with Antique Brown. (Caution: paler external margin of brownish may be lost with feather wear) *M. venezuelensis* (p. 488)
- 5A— Not as in 5 above
- 6 — Crown gray anteriorly, becoming darker posteriorly, the darker posterior crown strongly contrasting with the paler back *M. phaeocephalus* (p. 540)
- 6A— Not as in 6 above
- 7 — Smaller, and outer rectrices never with outer vanes whitish and noticeably paler than the inner vanes; or, if larger, back is Greenish Olive and contrasts strongly with uniformly blackish crown. *Males*: wing length usually shorter than 85 mm. and rarely as long as 86 mm.; tail length usually shorter than 78 mm. and rarely longer than 79 mm. *Females*: wing length usually shorter than 81 mm. and rarely longer than 82 mm.; tail length usually shorter than 73 mm. and rarely as long as 75 mm. *M. tuberculifer* (p. 449)
- 7A— Larger than characterized in 7 above, and never with Greenish Olive back contrasting strongly with uniformly blackish crown
- 8 — Tail shorter, relative to length of wing; ratio of tail length to wing length usually 92 percent or less (down to 81%) and rarely more than 93 percent; wing more pointed: ninth primary usually at least 1 mm. longer than fifth (up to 8 mm. longer), and rarely shorter than fifth; fourth primary usually no more than 5 mm. longer than tenth (may be as much as 4 mm. shorter), and rarely more than 6 mm. longer than tenth *M. swainsoni* (p. 498)
- 8A— Tail longer, relative to length of wing; ratio of tail length to wing length usually 93 percent or more (may exceed 100%), and rarely less than 91 percent; wing more rounded: fifth primary usually equal to or longer than ninth (up to 5 mm. longer), and rarely as much as 1 or 2 mm. shorter than ninth; fourth primary usually at least 5 mm. longer than tenth (up to 13 mm. longer), and rarely less than 4 mm. longer than tenth
- 9 — Outer pair of rectrices with outer vanes whitish and noticeably paler than the inner vanes; greater and median upper wing coverts broadly tipped with whitish *M. cephalotes* (p. 547)
- 9A— Not as in 9 above
- 10 — Crown and back lighter, closer to Brownish Olive
..... *M. panamensis* (p. 555)
- 10A— Crown and back darker, closer to Fuscous
..... *M. ferox* (p. 563)

VOCAL RESPONSE TO INTRUDING CONSPECIFICS

The following key utilizes only those vocal characters that constitute the normal response

of each species of South American *Myiarchus* to intruding conspecifics. This vocal response can be evoked by playback of the appropriate species-specific vocalizations. The terminology is defined in general terms in the Analysis of

rectrices; stripe of Fuscous (separating Antique Brown from the rachis) is less than 2.0 mm. wide in *crinitus* and more than 2.0 mm. wide in *tyrannulus*.

Vocal Characters and in detail under each of the species accounts. The reader may find it helpful to refer to figure 2, particularly if there are recordings or sound spectrograms of the

vocal response of the "unknown" species to encounters with conspecifics. A page reference is given for a more complete description of the vocal characters of each species.

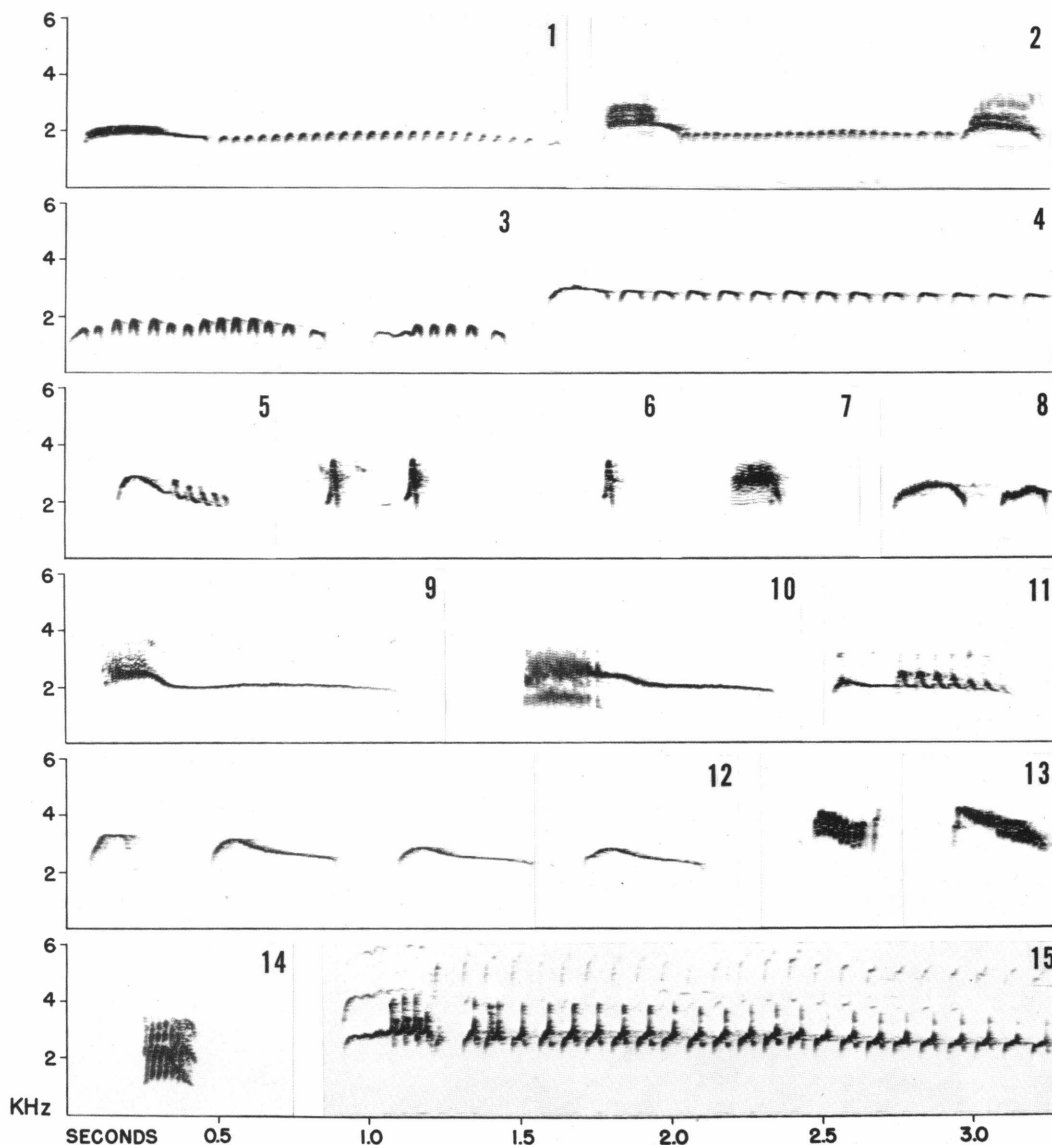


FIG. 2. Variation in vocal characters that constitute vocal response of South American *Myiarchus* to intruding conspecifics: rolls in association with rasps, 1, 2; rolls not in association with rasps, 3, 4; "wheel-r-r" notes, 5, 11; "huit" notes, 6; rasps, 7, 8; rasp-whistles, 9, 10; series of descending whistles, 12; rasping whistles, 13, 14; rattle, 15. Figure to be used with key on p. 446. See Appendix for field and catalogue data on these and all subsequent spectrograms.

- 1 — A conspicuous and consistent feature of the vocal response is the roll, defined here as a multi-syllabled call resulting from a rapidly delivered series of pulsed or discontinuous renditions of the carrier frequency; the traces of the syllables are variable, but always simple and chevron-like (fig. 2:1-4)
- 2 — Rolls normally are closely associated or even continuous with rasps, defined here as noisy, grating calls produced when the carrier frequency is modulated at frequencies in excess of 70 Hz.; displays made with the narrow-band filter reveal side-bands (oriented horizontally) rather than vertical oscillations (fig. 2:1 and 2)
- 3 — Vocal response includes "wheer-r-r" notes, as in figure 2:5, which are high-pitched calls produced when a sharp whistled note becomes modulated at a moderate frequency of 10 to 20 Hz.; normal response consists of repeated hiccups, rasps, rasp-rolls, and "wheer-r-r" notes *M. tuberculifer* (p. 456)
- 3A— No "wheer-r-r" notes, as in figure 2:5; normal response consists of repeated hiccups (except in *ferocior*), rasps, rasp-rolls, and rolls *M. swainsoni* (p. 507)
- 2A— No rasps, as defined above and illustrated in figure 2:1 and 2
- 4 — Rolls as in figure 2:3, normally without an introductory whistled note and delivered in long bouts and often without the intervention of other types of calls; normal response consists of repeated rolls, hiccups, and series of whistled notes *M. apicalis* (p. 535)
- 4A— Rolls normally with an introductory whistled note, as in figure 2:4, and not delivered in long bouts; normal response consists of repeated hiccups, rasping whistles, and rolls ...
..... *M. panamensis* (p. 557)
- 1A— No rolls, as defined above and illustrated in figure 2:1-4
- 5 — A conspicuous and consistent feature of the vocal response is the "huit" call, defined here as a brief rendition of the carrier frequency that is displayed graphically as a chevron-like note or as the ascending segment of a chevron and often delivered in series (fig. 2:6)
- 6 — Rasps, as defined in 2 above, are a conspicuous and consistent feature of the vocal response, and typically involve a pronounced deviation from the carrier frequency (fig. 2:7); normal response consists of "huit" notes, rasps, and slowly modulated whistles (vibrato) *M. tyrannulus* (p. 593)
- 6A— Rasps are not a conspicuous and consistent feature of the vocal response and, when present, reveal only moderate deviation from the carrier frequency (fig. 2:8); normal response consists of "huit" notes, slowly modulated whistles (vibrato) and some rasps .
..... *M. magnirostris* (p. 605)
- 5A— "Huit" calls, as defined above and illustrated in figure 2:6, are not a conspicuous and consistent feature of the response and, if present, are never delivered rapidly in series
- 7 — Response includes rasps, as defined in 2 above, and rasp-whistles, defined here as a rasp in which the carrier frequency is continued without interruption as an unmodulated whistled note, as illustrated in figure 2:9, 10
- 8 — Response includes "wheer-r-r" notes, as defined in 3 above, and illustrated in figure 2:11; normal response consists of repeated hiccups, rasps, rasp-whistles, and "wheer-r-r" notes *M. venezuelensis* (p. 492)
- 8A— No "wheer-r-r" notes, as in figure 2:11, but response includes a series of whistles in which the introductory whistle normally is sharp and piercing in quality and the remaining whistles become progressively more plaintive as they drop in frequency, amplitude, and frequency excursion (fig. 2:12); normal response consists of series of descending whistles, rasps, rasp-whistles, and hiccups (only in nominate *cephalotes*)
..... *M. cephalotes* (p. 550)
- 7A— No rasps and rasp-whistles, but response includes rasping whistles, modulated at frequencies from 40 to 60 Hz. (displays with narrow-band filter reveal vertical oscillations rather than horizontal side-bands, as in fig. 2:13, 14)
- 9 — Response includes rattles, defined here as prolonged, strident calls of complex syllables, as in figure 2:15; normal response consists of repeated hiccups, rasping whistles, and rattles *M. ferox* (p. 570)
- 9A— No rattle, as defined above
- 10 — Rasping whistles regularly involve frequencies as low as 1 and 2 kHz. (fig.

- 2:14); normal response consists of repeated hiccups, rasping whistles, and high-pitched whistles *M. phaeocephalus* (p. 540)
- 10A— Rasping whistles involve frequencies principally above 3 kHz. and never below 2 kHz. (fig. 2:13); normal response consists of repeated rasping whistles and hiccups *M. semirufus* (p. 584)

DAWN SONG

The following key utilizes only those vocal characters that constitute the dawn song of each species of South American *Myiarchus*, as defined in general terms in the Analysis of Vocal Characters and in detail under each of the spe-

cies accounts. The reader may find it helpful to refer to figure 3, particularly if there are recordings or sound spectrograms of the dawn song of the "unknown" species. The dawn song of *Myiarchus apicalis* is unknown, hence that species has been omitted here.

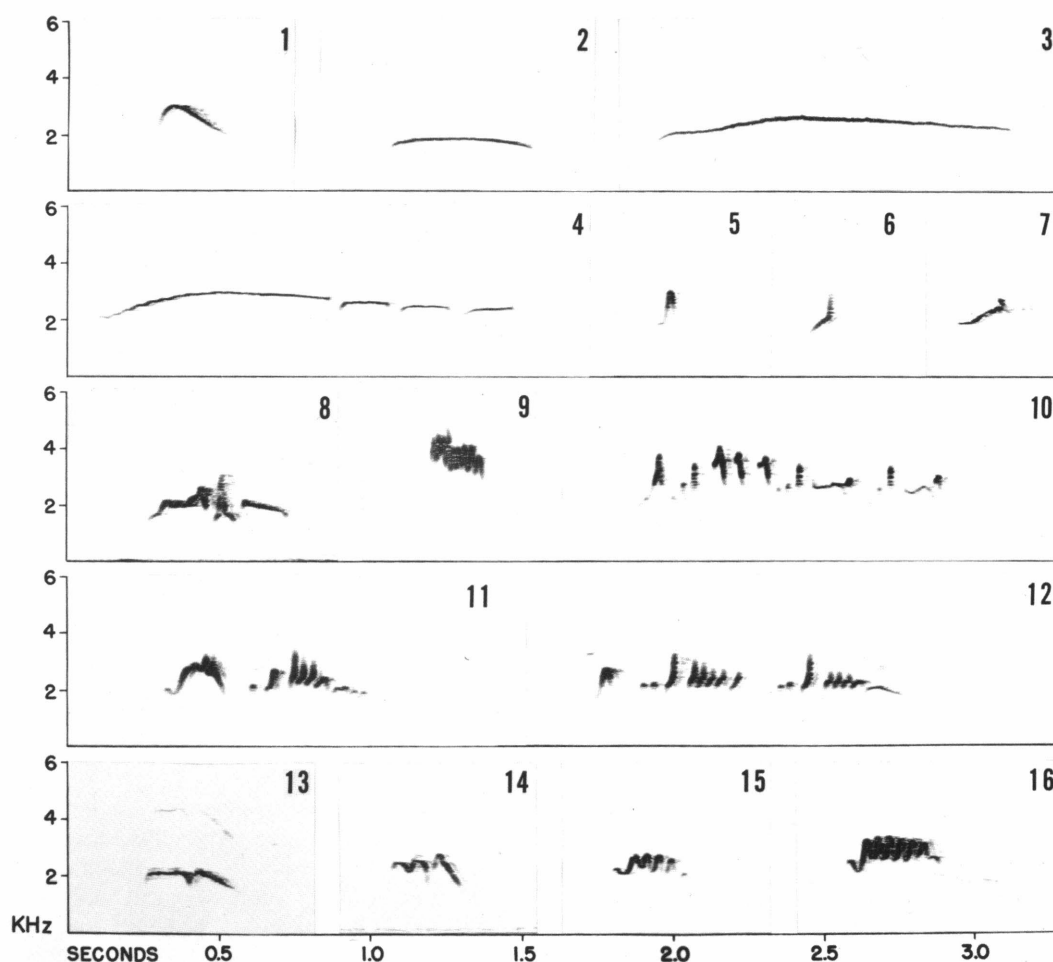


FIG. 3. Variation in vocal characters that constitute dawn songs of South American *Myiarchus*: simple, whistled notes, 1-4; "huit"-like notes, 5-7; complex phrases, 8, 10-12; rasping whistle, 9; slowly but definitely modulated whistles (vibrato), 13-16. Figure to be used with key on p. 448.

- 1 — Dawn song includes simple, virtually unmodulated whistled notes that may be either plaintive and of prolonged duration or rather sharp and piercing in quality; displays of these whistles reveal a gentle to moderate frequency excursion (fig. 3:1-4)
- 2 — Whistles alternated or associated with "huit"-like notes (fig. 3:5-7) and/or longer, more complex phrases consisting of a central "huit"-like syllable and introductory and terminal syllables of longer duration and variable modulating frequency (fig. 3:8)
 - 3 — Whistles and "huit" notes alternated or associated with more complex phrases as identified in 2 above (fig. 3:8) some *M. swainsoni* (p. 508)
 - 3A— Whistles alternated or associated with "huit" notes only *M. tuberculifer* (p. 456) and some *M. swainsoni* (p. 508)
- 2A— Whistles only
 - 4 — Whistles uniformly rather sharp and piercing in quality, due to their short duration (less than 0.25 second) and prominent frequency excursion (fig. 3:1) . *M. cephalotes* (p. 552)
 - 4A— Whistles more plaintive and prolonged (longer than 0.25 second and often longer than 0.5 second), with only a slight frequency excursion (fig. 3:2-3)
 - 5 — Whistles uniformly longer than 0.5 second and rendered at intervals of several seconds *M. venezuelensis* (p. 492)
 - 5A— Whistles of variable duration, but typically in a series, with an introductory more prolonged whistle (0.5 second or longer) followed in rapid succession by a number of shorter whistles on a scale of slightly decreasing frequency (fig. 3:4) *M. phaeocephalus* (p. 543)
- 1A— Dawn song includes no simple, virtually unmodulated whistles as defined in 1 above and illustrated in figure 3:1-4
 - 6 — Dawn song consists exclusively of isolated and slowly but definitely modulated whistled notes (vibrato), as in figure 3:13-16
 - 7 — Isolated whistles typically modulated at a slower frequency (up to 15 Hz.), as in figure 3:13 or 14 *M. panamensis* (p. 560)
 - 7A— Isolated whistles typically modulated at a faster frequency (15 to 30 Hz.), as in figure 3:15 or 16 *M. ferox* (p. 570)
 - 6A— Not as in 6 above
 - 8 — Dawn song includes isolated rasping whistles, modulated at a frequency of 45 to 60 Hz. (fig. 3:9) *M. semirufus* (p. 584)
 - 8A— Not as in 8 above
 - 9 — Complex phrases, as in figure 3:10, in which the rapid "huit" notes reveal a prominent glissando in the descending segment of each "huit" component *M. magnirostris* (p. 605)
 - 9A— Complex phrases, as in figure 3:11 or 12, in which the rapid "huit" notes reveal a prominent glissando in the ascending segment of each "huit" component *M. tyrannulus* (p. 594)

SPECIES ACCOUNTS

Some general comments on the material covered in the species accounts, the basis for the sequence of species followed here, and the justification for the descriptive detail on vocal characters were included in the Introduction.

Each species account contains a brief introductory statement on the geographical range of the species that also identifies, in a cursory way, any unique or unusual features of distribution or geographical variation to be discussed in detail later. There follows a summary state-

ment as to how my taxonomic treatment differs from current usage, and I list those subspecies, if any, that are admitted here. Specific diagnoses include both morphological and vocal characters. The discussions of habitat are illustrated with photographs selected to represent the variety of habitats known to be occupied by each species.

Except for four species for which we have no data, all *Myiarchus* are known to nest normally in cavities in trees or the equivalent.

There are only four other genera, among the more than 100 genera of tyrannid flycatchers, in which nesting in tree-cavities is the rule. *Myiarchus* is the *only* genus in which the species typically include quantities of soft fur, feathers, paper, and shed reptilian skin in the nest lining. These behavioral patterns are of considerable value, therefore, in helping diagnose the genus and in setting its limits. For these reasons I have included my own observations on the breeding biology of these species and have cited the pertinent literature that has come to my attention. The discussions of the timing of breeding and of the annual, complete molt are particularly important in considerations of geographical variation within the wide-ranging species and in differentiating between resident and migrant forms.

A detailed itinerary of fieldwork is included with each species account.

The synonymies are not meant to be complete, but do include the senior synonym (and type locality), all junior synonyms, the first usage of new combinations of old names, as well as the combinations used in a few standard

references, faunal treatises, and monographs.

For each subspecies or monotypic species there is a more detailed discussion of distribution, a map with the localities of specimens examined and of the sites where I studied the taxon in the field, and a list of these localities, by country. In the list of localities, each locality is followed by a comma and the name of the department or province in which it is located, and localities are separated by semicolons. When two or more localities are within 75 km. of one another, only one has been plotted on the accompanying map; the additional localities have been placed in parentheses in the list, and the department or province is given only if different from that of the locality with which they are associated.

There are detailed discussions for many of the taxa that relate to geographical variation, the bases for synonymies, and relationships to other taxa. In the latter discussions I frequently report the results of my standardized playback experiments, in so far as they contribute to an understanding of relationships.

MYIARCHUS TUBERCULIFER (D'ORBIGNY AND LAFRESNAYE)

Myiarchus tuberculifer is the most widely distributed species of the genus, geographically and ecologically, and is the only species that occurs throughout Middle America and most of northern South America without a major hiatus in range. In South America the range occupies most of the tropical and subtropical zones: west of the Andes to southern Ecuador, the subtropical Andes south to the temperate zone of northwestern Argentina, and east of the Andes to central Bolivia and central eastern Brazil, but lacking in the more xeric regions of south-central and eastern Brazil (fig. 4).

The species is polytypic, with five subspecies (*tuberculifer*, *pallidus*, *brunneiceps*, *nigriceps*, and *atriceps*) recognized here, and most, if not all, populations are nonmigratory (see p. 470).

The population (*barbirostris*) on Jamaica in the West Indies has been considered by Zim-

mer (MS) and Bond (1956, 1967) as conspecific with *M. tuberculifer*, but I have argued (Lanyon, 1967) for full specific status for that insular form and for placing it in a superspecies with *M. [barbirostris] tuberculifer*.

In addition to its wide distribution, *M. tuberculifer* is also unique within the genus in the degree to which it exhibits geographical variation in body size, plumage coloration, and vocal characters. Of particular interest is the fact that the South American subspecies are arranged in a circular manner, with reproductive isolation nearly but not quite complete at the southern end of this "open ring" (fig. 4). A special section has been devoted to a discussion of the evidence for this isolation and for limited interbreeding between the extreme forms.

DIAGNOSIS: Rectrices of adults not conspicuously marked with Antique Brown or with whitish edges or tips. Smaller than other "dark-

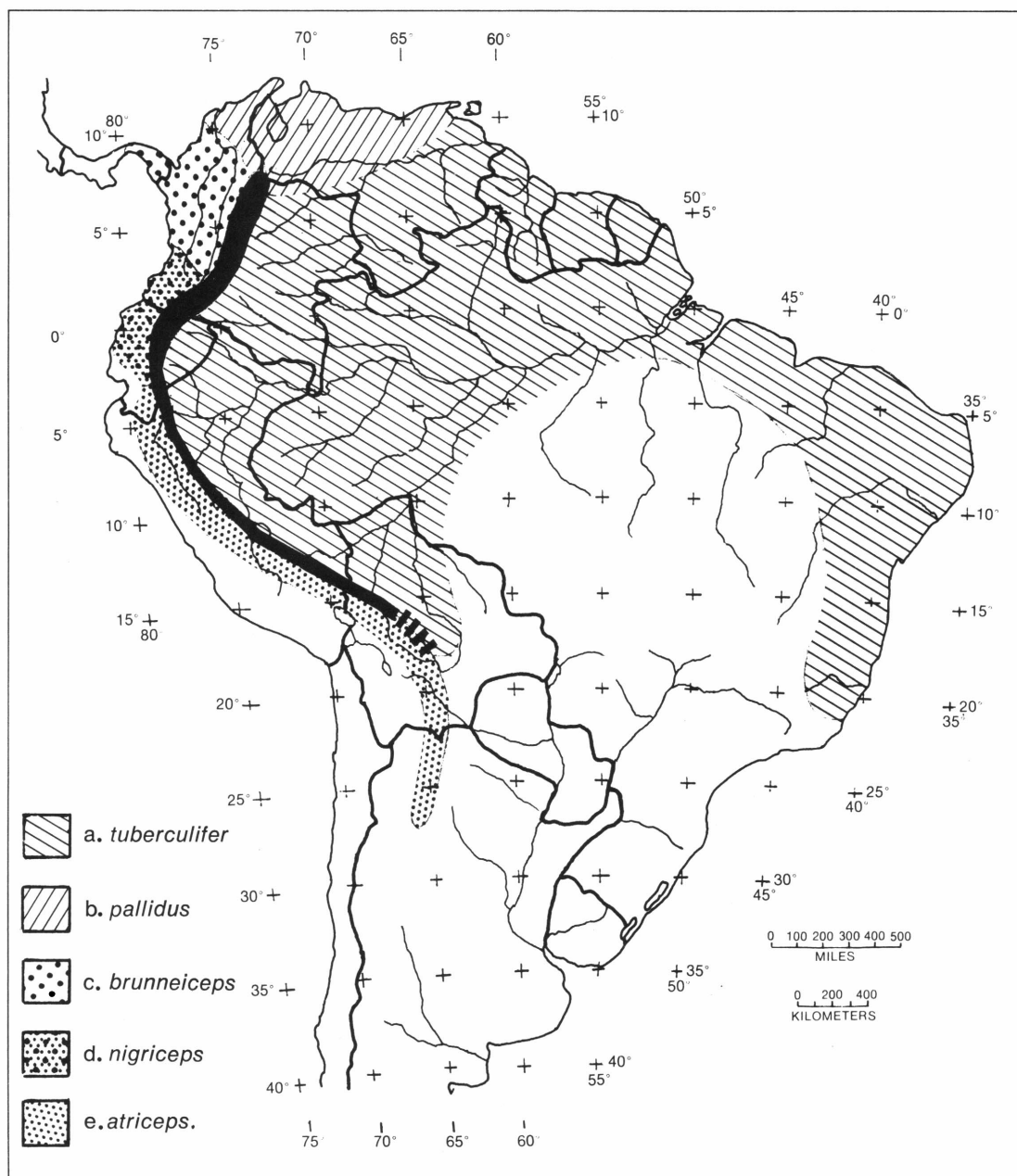


FIG. 4. Diagrammatic representation of circular distribution of subspecies of *Myiarchus tuberculifer*. Physical and ecological barriers (wide black zone) effectively isolate *tuberculifer* from *brunneiceps* and *nigriceps*, and asynchronous breeding cycles are a barrier (narrow black zone) to interbreeding between *atriceps* and *tuberculifer* from southern Ecuador to Bolivia. Broken black zone in Bolivia indicates a region of known interbreeding between *atriceps* and *tuberculifer*.

tailed" species. *Males*: wing length usually shorter than 85 mm. and rarely as long as 86 mm.; tail length usually shorter than 78 mm. and rarely longer than 79 mm. *Females*: wing length usually shorter than 81 mm. and rarely longer than 82 mm.; tail length usually shorter than 73 mm. and rarely as long as 75 mm. If larger (*atriceps*), back is Greenish Olive and contrasts strongly with uniformly blackish crown. In fresh specimens, entire mandible black (no seasonal or geographical variation) and color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics includes repeated rolls closely associated with rasps and "wheer-r-r" notes. Dawn song consists of plaintive whistles alternated with "huit" notes.

HABITAT (FIGS. 5-7, 29, 54, 59, 63): The species is found over a greater altitudinal range than that of any other *Myiarchus*, from sea level to 3400 m. (temperate zone). One of the subspecies (*nigriceps*) is known to range from sea level to 2400 m. Although the species may be found in such habitats as coffee plantations, wooded areas along rivers and streams, and in disturbed agricultural areas, like most species of *Myiarchus*, it has penetrated more heavily forested regions to a greater degree than any other member of the genus. When found in habitats dominated by tall, mature trees, *M. tuberculifer* spends most of its time in the tree canopy and is reluctant to descend to the shrub or smaller tree level even in response to playback. Wetmore (1972) recorded the species in Panama as inhabiting "tree cover at the borders of fields and pastures, the inner margins of mangrove swamps, and scattered open growth. They penetrate heavily forested areas mainly along the open courses of larger streams. They may remain in areas of shifting agriculture, in the quickly established second growth that fills cleared areas used temporarily for plantations." To these observations I add, from my own field experiences, alder woodlands in the temperate zone of southern Bolivia and northern Argentina, banana plantations in the tropical Pacific lowlands of Ecuador, coffee plantations in the upper tropical zone of the interior valleys of

Peru, subtropical forests throughout the Andes and Venezuela's northern cordillera, and tropical rain forest in the Amazon basin.

BREEDING AND ANNUAL CYCLE: The species is a cavity nester and uses nesting materials similar to those of other members of the genus. I found no nests of the South American forms but I have observed nests of the species extralimittally: (1) in a knothole, 10 m. up in a sycamore (*Platanus* sp.) near Portal, Arizona; (2) in a natural cavity 12 m. up in a dead stub, near Barranca, Puntarenas, Costa Rica; (3) in a woodpecker cavity 5 m. up in a dead stub near San José, Escuintla, Guatemala, and (4) in the darkened recesses of dead fronds 10 m. up in a date palm near Tapachula, Chiapas, Mexico. Skutch (1960) recorded three nests from Honduras and Guatemala, two placed in hollows formed by decay in fence posts and the third in a deep hole in the broken top of a leaning tree trunk. All three nests were of soft vegetable materials, hair and feathers, and one contained a fragment of snake skin.

I have found only two references to the nests of the South American forms. Belcher and Smooker (1937) reported that *tuberculifer* in Trinidad used the same hole in a dead stump, about 4.5 m. from the ground, for a nest site in two consecutive years. The nest was of "dried weed-stems and moss, and lined with thin black horsehair-like fibres strongly woven together." Wetmore (1972) has observed *brunneiceps* in Panama gathering feathers for use in nests in a "tree cavity 10 meters above the ground" and in a "hole in a stub."

The breeding season for *pallidus*, *brunneiceps*, and *nigriceps* extends from March through June. Wetmore (1972) wrote of *brunneiceps* in Panama: "Nesting appears to begin in March and April." I collected a pair of *pallidus* in Venezuela in early May of which the female was carrying eggs in the oviduct and the male had testes measuring 12 by 6 mm., and I have seen specimens of juvenals from April through July. In Colombia, prebreeding *nigriceps* in mid-February had testes measuring only 4 by 2 mm., whereas the testes of males taken in late March and mid-April measured 11 by 6 mm. I recorded a male giving dawn song

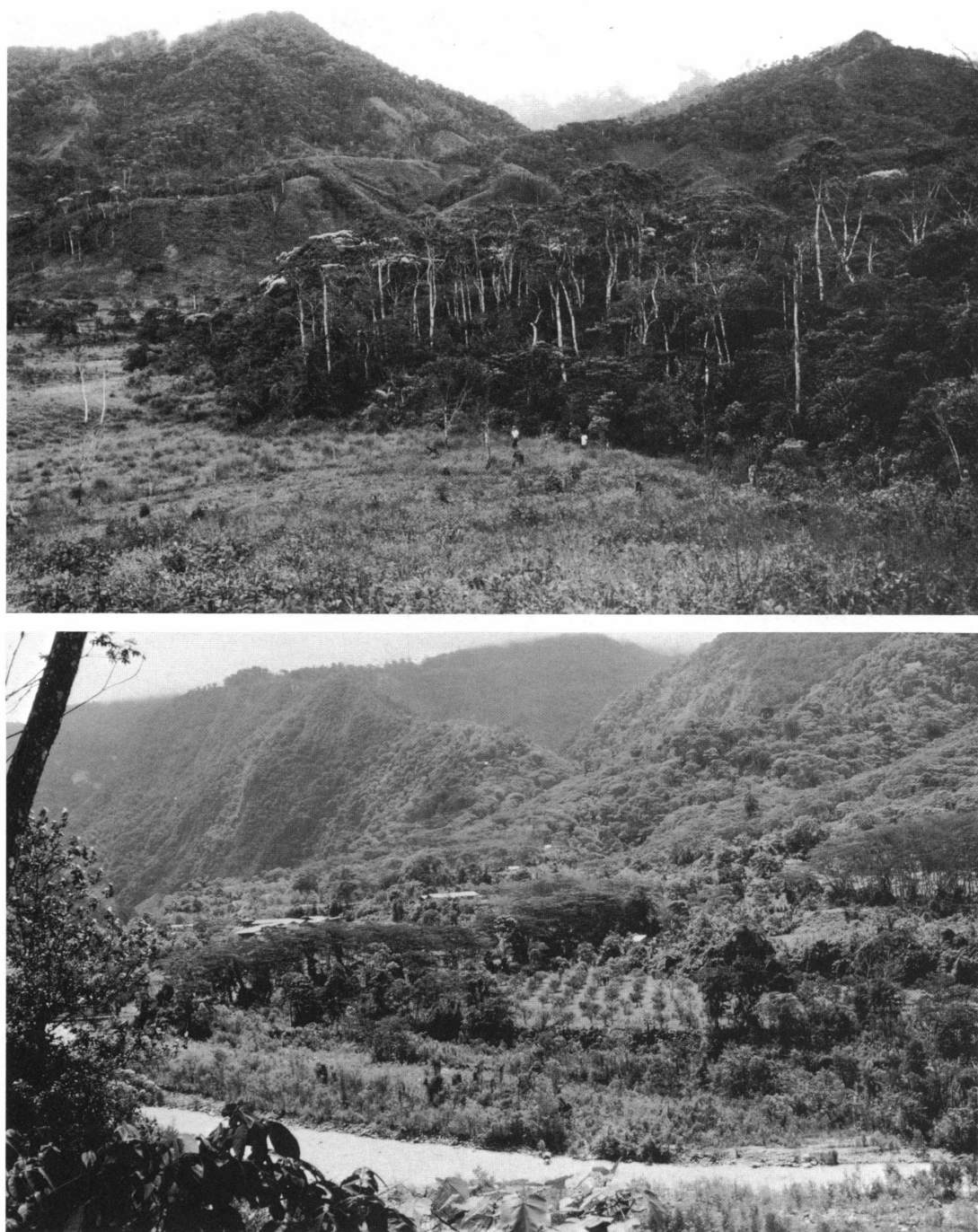


FIG. 5. Habitat of *Myiarchus tuberculifer tuberculifer*. *Top*: Clearings in humid tropical forest in south-eastern Ecuador, near Zamora, January 1974; elevation 900 m. *Bottom*: Coffee plantation in lower subtropical zone of central Peru, near San Ramón, Junín, November 1972; elevation 1000-1500 m. *M. t. atriceps* is resident form at higher elevations in the Andes.



FIG. 6. *Top*: Habitat of *Myiarchus tuberculifer pallidus* in clearings in humid subtropical forest at Rancho Grande, Aragua, Venezuela, May 1968; elevation 1000 m. *Bottom*: Habitat of *M. t. nigriceps* in open subtropical woodland near Popayán, Cauca, Colombia, March 1973; elevation 2000 m. Sympatric with *M. c. cephalotes* at this locality.

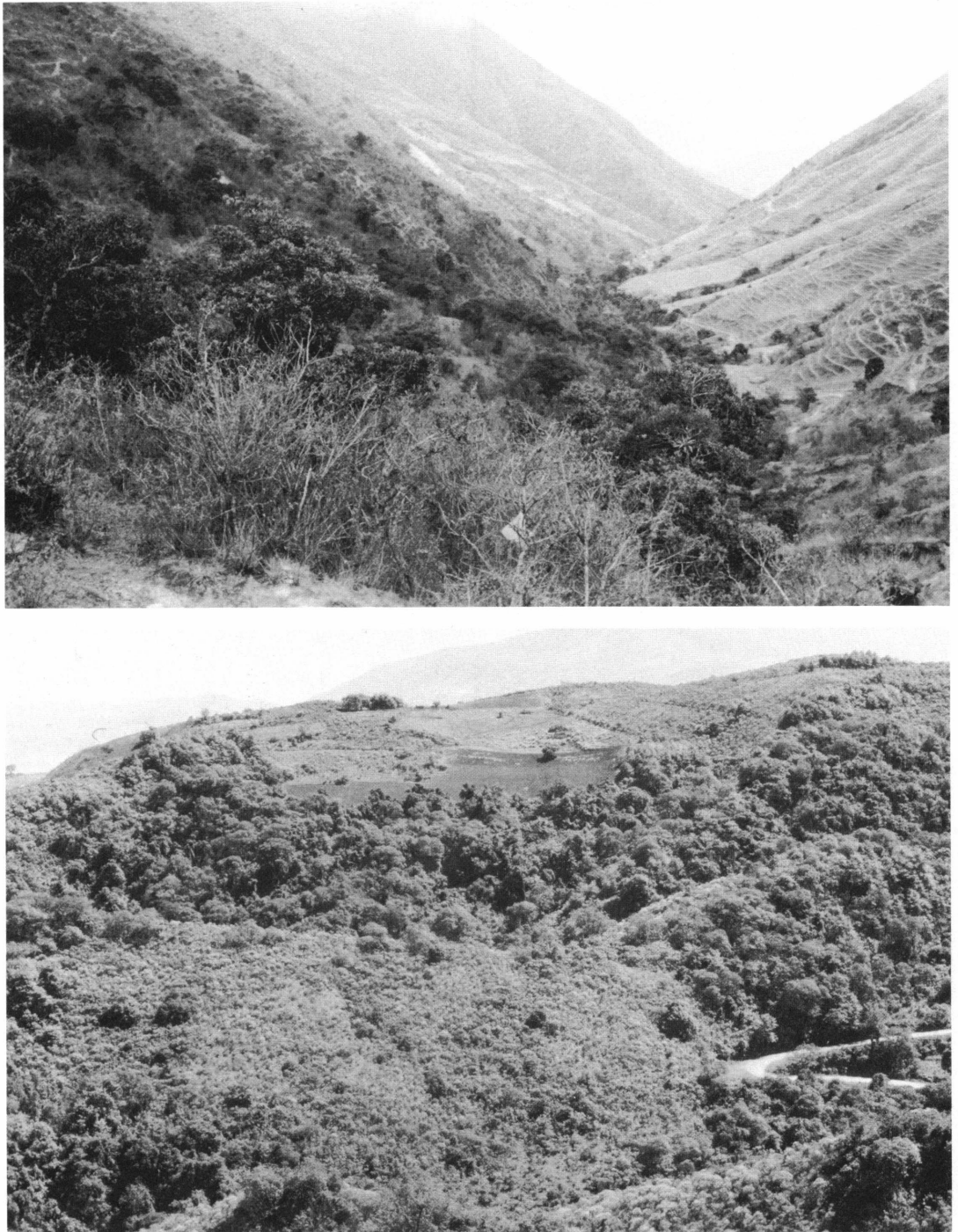


FIG. 7. Habitat of *Myiarchus tuberculifer atriceps*. *Top*: Low, open subtropical woodland on the Pacific slope of the Abra de Porcula, Piura, Peru, December 1973; Pacific and Amazonian drainages meet here at an elevation of only 2100 m. *Bottom*: Alder forest in humid temperate zone near Tucumán, Argentina, November 1967; elevation 1300 m.

at Popayán, Colombia, on March 31. I have seen no specimens of *nigriceps* from Ecuador that have breeding data, but molt data and the small size of testes of specimens taken in other months suggest that Ecuadorian *nigriceps* breed on approximately the same schedule as the Colombian birds.

Molt data and gonad size in specimens taken at other times during the year establish that the breeding season of nominate *tuberculifer* in the Amazon basin and along the eastern edge of the Andes extends from August to October, in approximate synchrony with that of *M. f. ferox*, another widespread Amazonian form. An Ecuadorian specimen taken in July had very small testes, as did one taken in Surinam in December (in mid-prebasic molt). Another from Loreto, Peru, had quite an enlarged ovary on August 3. A series taken in Junín, Peru, in mid-November had finished breeding and were undergoing the prebasic molt.

The shift in the breeding season from August to October throughout the Amazon basin to March through June in the subspecies of northwestern South America does not occur in the zone of contact between *tuberculifer* and *pallidus* (fig. 4), as one might expect, but in some as yet undetermined part of the range of *tuberculifer* somewhat farther to the southeast. The northernmost populations of *tuberculifer*, in Trinidad and southeastern Venezuela, though closer to the nominate form morphologically, have an annual cycle like that of *pallidus*. Specimens taken in May in Bolívar, Venezuela, have enlarged testes and active brood patches, and juvenals have been taken as early as April. Belcher and Smooker (1937) found active nests on Trinidad in April and June, and Chapman (1894) collected a laying female on Trinidad on April 24.

The southernmost populations of *atriceps*, in the Andes of Argentina and Bolivia, breed from mid-November through December and breeding activity appears to be rather well synchronized as is usually the case in temperate latitudes (and altitudes). Males taken in late October and early November have testes that average 9 by 4 mm., whereas the testes of males taken in mid-November and early December average 11 by 6 mm. in size. Females

taken in mid- and late November have been noted as having enlarged ova, "already laid," or "egg in oviduct." Presumably *atriceps* in southern Peru breed on a similar schedule, i.e., in November and December, though I have seen no males taken during the critical months of September through March. A good series of males from Junín, Peru, in April and May are in fresh plumage and marked as having testes not enlarged.

Farther northward in the Andes there is a shift in the annual cycle of *atriceps*, probably beginning somewhere in central Peru. Specimens of *atriceps* taken in Piura, Peru, in late December have testes measuring only 2 by 1 mm., and they exhibit a light prealternate molt. Other specimens of *atriceps* taken in northern Peru from late May to August are in various stages of prebasic molt and have equally small testes. These data suggest a breeding season in northern Peru from February through April.

The clinal shift in the breeding season of *atriceps* continues into southern Ecuador, where the available data suggest breeding from March through June. Specimens taken in mid-January have small testes and exhibit prealternate molt, while specimens taken in September and October are either in fresh plumage or late stages of prebasic molt. Juvenals have been taken in late July.

The definitive plumage is replaced during a complete annual molt that immediately follows breeding. Since there is considerable geographical variation in the timing of the breeding season, there is a comparable variation in the timing of the complete or prebasic molt. The prebasic molt in *pallidus*, *brunneiceps*, and *nigriceps* takes place from June through October. The plumage in these forms is fresh, i.e., least worn, from October through December. Nominate *tuberculifer* throughout the Amazon basin and along the eastern edge of the Andes undergoes the prebasic molt from October through March. The northernmost populations of *tuberculifer*, in Trinidad and southeastern Venezuela, have a molt schedule like that of *pallidus*. The clinal shift in the breeding season of *atriceps* is matched by a similar shift in the timing of the prebasic molt. Argentine and Bolivian populations undergo a complete molt

in January and February. In northern Peru, *atriceps* does not renew the remiges and rectrices until later in the year, from May through August. In southern Ecuador, this same molt occurs from July through October.

I have presented evidence (Lanyon, 1975b) that suggests that at least some populations (*nigriceps*) of this species undergo an incomplete prealternate molt from one to two months prior to the onset of breeding. In the Cauca valley of Colombia, this partial molt occurs in February and March. Subsequently I collected specimens of *atriceps* in southern Ecuador in mid-January and these birds were not yet sexually active but were undergoing slight prealternate molt. It is probable that appropriate material will reveal a similar prealternate molt in other populations of this species.

VOCAL CHARACTERS: The analysis of vocal characters of *M. tuberculifer* is based on recordings from these samples:

M. t. brunneiceps—Panama, two pairs

M. t. pallidus—Venezuela, seven pairs

M. t. nigriceps—Colombia, five pairs; Ecuador, two pairs

M. t. atriceps—Ecuador, two pairs; Peru, six pairs; Bolivia, four pairs; Argentina, nine pairs.

M. t. tuberculifer—Venezuela, five pairs; Surinam, one pair; Colombia, one pair; Peru, two pairs; Bolivia, three pairs.

Intergrades between *M. t. tuberculifer* and *M. t. atriceps*—Bolivia, four pairs.

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1 and illustrated in figures 8 to 11.

In response to playback, or when excited by intruding conspecifics, *M. tuberculifer* vocalizes with repeated hiccups, rasps, rasp-rolls, and "wheer-r-r" notes. The hiccups in my sample were somewhat variable in configuration, as illustrated by the examples graphed in figure 8:10-21. Typically, the first syllable is a very brief, "huit"-like note, whereas the second and accented syllable is of longer duration, greater amplitude, and noticeably greater frequency excursion. Uncommonly, the two notes may be rendered as one continuous syllable, which illustrates the principle of a common carrier frequency. The rasp (fig. 9) may be rendered as

an isolated call, or as one call in a series or train of similar calls given rapidly in sequence, and sometimes as the introductory syllable that is then converted immediately into a roll (rasp-roll). There is less deviation from the carrier frequency than in the rasp of some conspecifics. The syllables of the roll (fig. 9) are of the chevron-type ("huit" notes) and they characteristically rise slightly in both carrier frequency and amplitude during the central portion of the call. Typically, the roll is introduced by a rasp or rasp-whistle, but it may be given as an isolated phrase as well. The "wheer-r-r" note (fig. 10) normally is a single syllable and is produced when the carrier frequency of a sharp whistled note becomes modulated at a moderate frequency of 10 to 20 Hz. Often it is rendered in close association with hiccups and rasps, and on occasion a bird will deliver a hiccup and "wheer-r-r" note as a continuous signal or may produce a continuous series of "wheer-r-r" notes.

Foraging birds not excited by playback or intruding conspecifics will deliver plaintive whistles (fig. 8) at intervals of several seconds. Presumably these calls serve as location notes in the communication between paired birds. In my samples whistles vary in length from 0.4 to 1.0 second and normally were gently slurred with very little frequency excursion. Occasionally, when terminating a whistle, a bird will change the frequency abruptly, producing a glissando effect (fig. 8:7, 9). Whistles often are given by an individual after the removal of its mate by collecting, and sometimes in response to the termination of playback (one or two minutes after the cessation of the tape recording).

DAWN SONG: The dawn song of the male of *M. tuberculifer* consists of alternated whistles and "huit" notes, as in figure 11. The whistles do not differ from those given by foraging birds during the daylight hours and include some that are plaintive in quality with little if any frequency excursion, and others that are accented with a pronounced glissando and increase in amplitude. Although the "huit" note was recorded in samples of dawn song from each of the five subspecies, and its presence appears to be the rule, nevertheless it was omitted on occasion in the recordings of two popu-

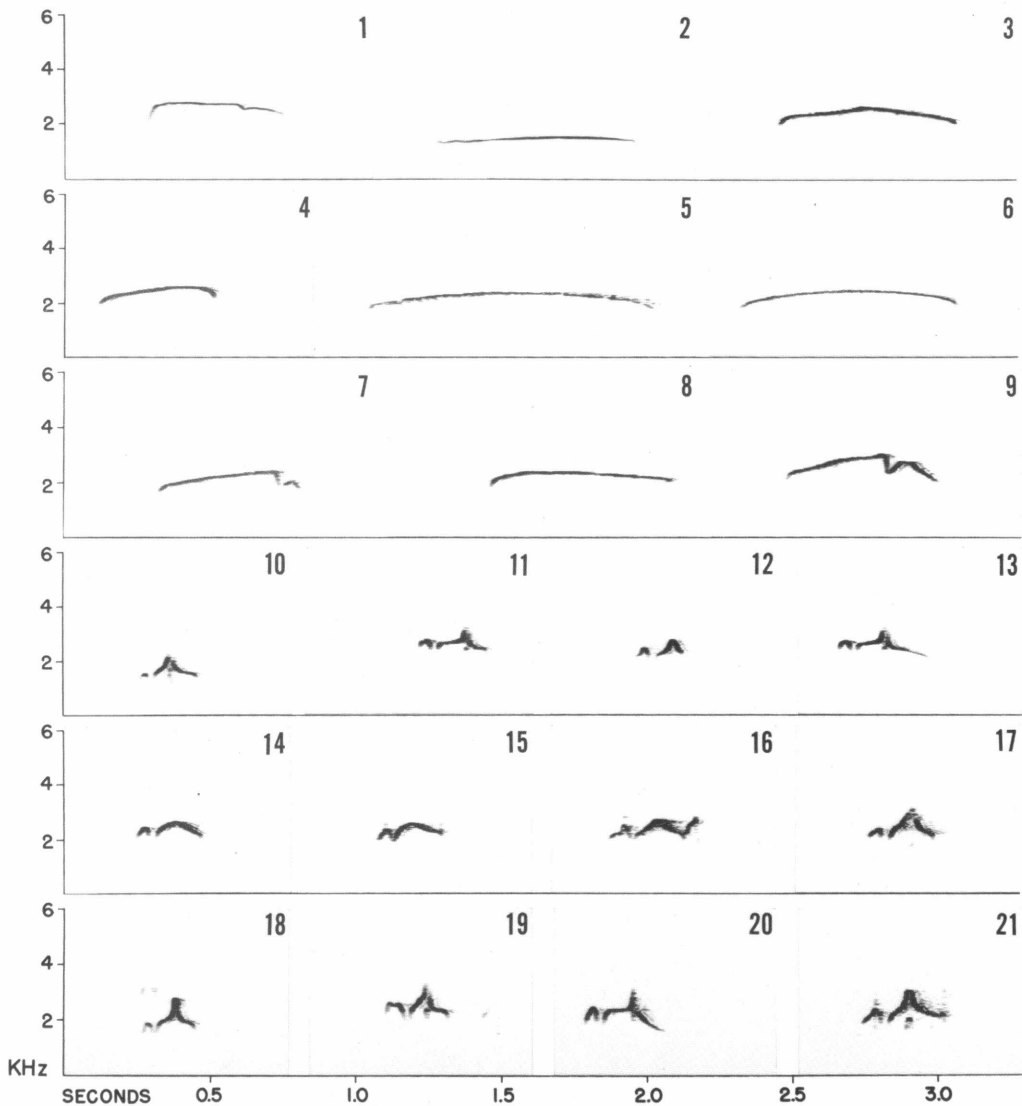


FIG. 8. Variation in vocal characters of *Myiarchus tuberculifer*: whistles (1-9) and hiccups (10-21). These spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. brunneiceps* (Panama, 1, 11, 13); *M. t. pallidus* (Venezuela, 8, 12, 14, 15); *M. t. nigricaps* (Colombia, 4, 20; Ecuador, 6); *M. t. atriceps* (Ecuador, 19; Peru, 7; Bolivia, 10; Argentina, 2, 18); *M. t. tuberculifer* (Venezuela, 5, 16; Surinam, 21); intergrades between *M. t. tuberculifer* and *M. t. atriceps* (Bolivia, 3, 9, 17).

lations. In those instances the whistles simply were alternated with one another without an intervening "huit."

GEOGRAPHICAL VARIATION: I could find no evidence for geographical variation in the vocal

characters of *M. tuberculifer* other than in the carrier frequency used to produce them. There is a strong inverse correlation between this carrier frequency and body size, as represented by wing length: larger birds produce a lower car-

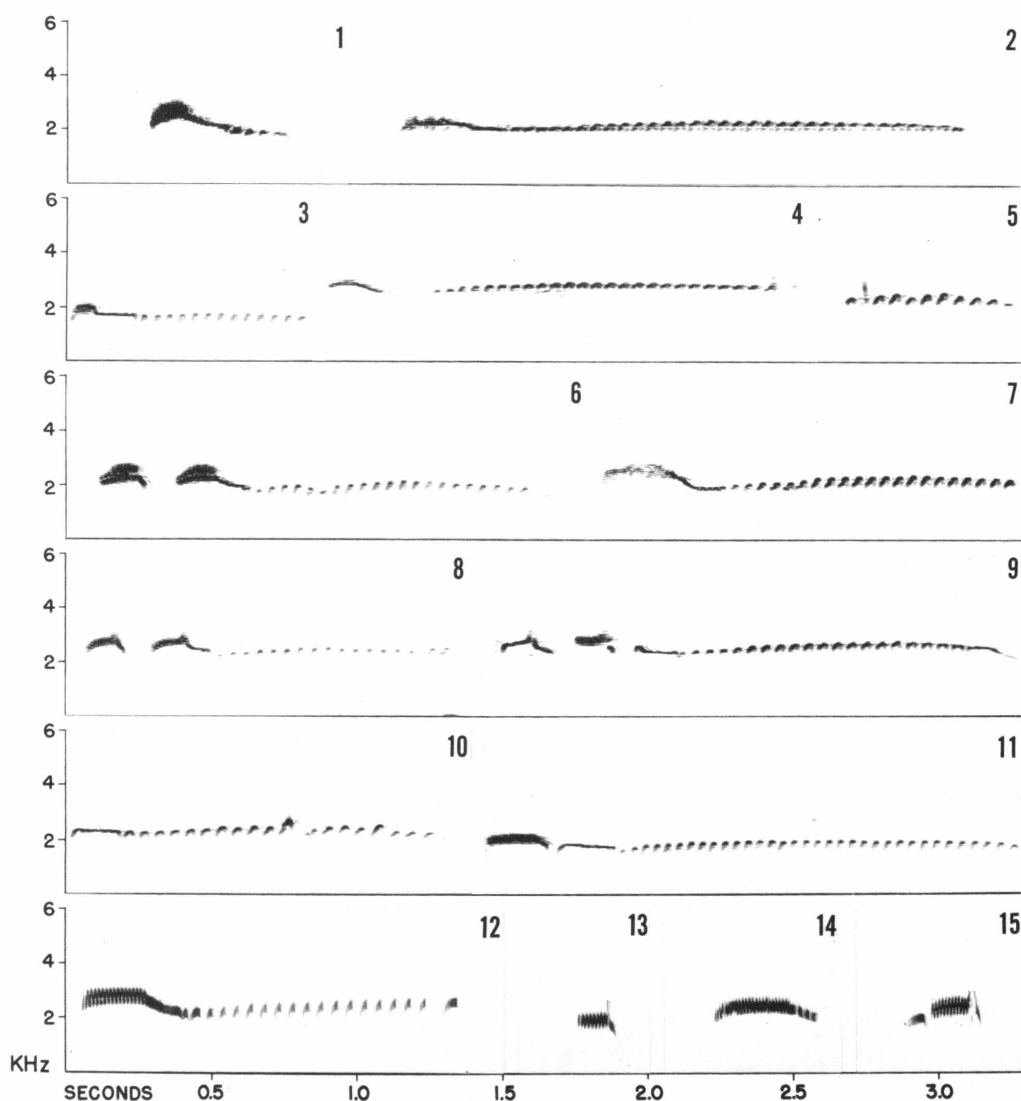


FIG. 9. Variation in vocal characters of *Myiarchus tuberculifer*: rasps and rolls. These spectrograms were made from recordings of the following populations: *M. t. brunneiceps* (Panama, 4, 9); *M. t. pallidus* (Venezuela, 8, 15); *M. t. nigriceps* (Colombia, 7); *M. t. atriceps* (Ecuador, 1; Bolivia, 11; Argentina, 3, 6, 13); *M. t. tuberculifer* (Venezuela, 5, 10; Surinam, 2; Peru, 14; Bolivia, 12). The 300 Hz. filter was used for 12 through 15 only.

rier frequency than do smaller birds (fig. 17). The significance of this correlation is discussed in greater detail in the section dealing with the relationship of *tuberculifer* and *atriceps* in Bolivia. The largest subspecies, *atriceps*, may use a carrier frequency as low as 1.3 kHz., whereas the smallest South American sub-

species, *brunneiceps*, may use one as high as 3.0 kHz.

ITINERARY OF FIELDWORK

1967—November 11-14, with *atriceps* near Tucumán, Tucumán, Argentina.

1968—April 30 through May 4, with *pallidus* at

- Rancho Grande, Aragua, Venezuela; May 13-14, with *pallidus* near Barinas, Barinas, Venezuela; May 17-18, with *pallidus* near San Fernando de Apure, Apure, Venezuela; May 20-21, with *tuberculifer* near El Palmar, Bolívar, Venezuela.
- 1969—April 17-21, with *brunneiceps* at Cerro Azul, Panamá, Panama; April 29 through May 6, with *tuberculifer* at Kavanayén, Bolívar, Venezuela; May 9-16, with *pallidus* near San Fernando de Apure again.
- 1970—May 2-4, with *tuberculifer* near El Palmar and Tumeremo, Bolívar, Venezuela; May 14-16, with *pallidus* near Cerro El Cedro, Zulia, Venezuela; May 25-26, with *tuberculifer* near Villavicencio, Meta, Colombia; November 29 through December 1, with *atriceps* near Tucumán again; December 20, with *tuberculifer* near Phedra, Surinam.
- 1972—November 4-9, with *atriceps* near Chinchao, Huánuco, Peru; November 10-15, with *tuberculifer* near San Ramón, Junín, Peru.
- 1973—March 9-13, with *nigriceps* near Popayán, Cauca, Colombia; March 25, with *nigriceps* near Queremal, Valle, Colombia; March 30-31, with *nigriceps* near Popayán again; December 22, with *atriceps* at Abra de Porcula, Piura, Peru.
- 1974—January 5, with *nigriceps* along the Río Palenque, Pichincha, Ecuador; January 7-11, with *atriceps* near Loja, Loja, Ecuador; April 20, with *nigriceps* near Popayán again; May 4, with *pallidus* near Cubiro, Lara, Venezuela; October 18-25, with intergrades between *tuberculifer* and *atriceps* in the Yungas of Cochabamba, Bolivia (above Villa Tunari); October 26, with *tuberculifer* near Villa Tunari, Cochabamba, Bolivia; October 31 and November 17, with *atriceps* near Pojo, Cochabamba, Bolivia; November 9, with

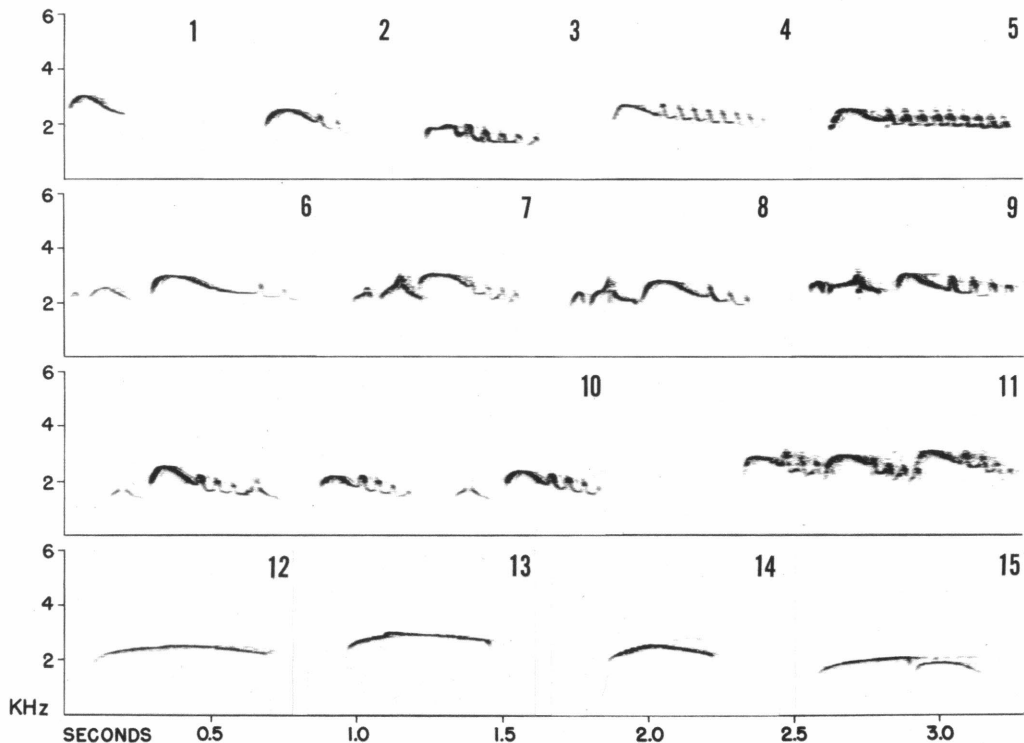


FIG. 10. Variation in vocal characters of *Myiarchus tuberculifer*: "wheeler-r" notes (1-11) and dawn song whistles (12-15). These spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. brunneiceps* (Panama, 9, 13); *M. t. pallidus* (Venezuela, 6, 14); *M. t. nigriceps* (Colombia, 5, 12); *M. t. atriceps* (Ecuador, 8; Bolivia, 3, 10; Argentina, 2, 15); *M. t. tuberculifer* (Colombia, 1; Surinam, 4; Peru, 7, 11).

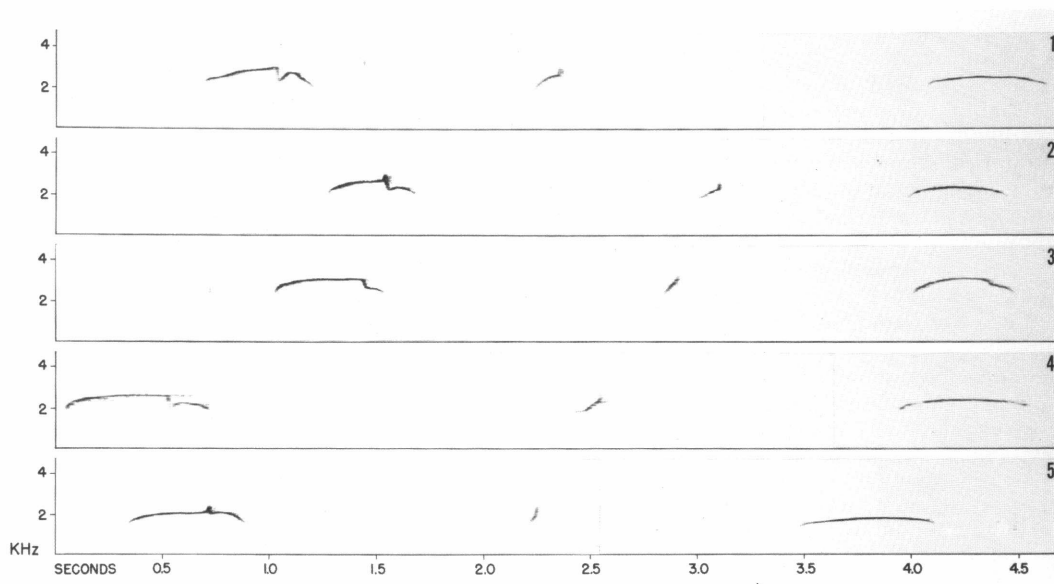


FIG. 11. Variation in vocal characters of *Myiarchus tuberculifer*: dawn song. These spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. brunneiceps* (Panama, 3); *M. t. pallidus* (Venezuela, 2); *M. t. nigriceps* (Colombia, 4); *M. t. atriceps* (Argentina, 5); *M. t. tuberculifer* (Bolivia, 1).

atriceps near Entre Ríos, Tarija, Bolivia; November 21, with *tuberculifer* near Yolosa, La Paz, Bolivia.

SYSTEMATICS

Myiarchus tuberculifer tuberculifer
(D'Orbigny and Lafresnaye)

Tyrannus tuberculifer D'Orbigny and Lafresnaye, 1837, p. 43 (type locality, Guarayos, Bolivia; holotype in Paris Museum).

Myiarchus tuberculifer: Cabanis, 1847, p. 248 (new combination).

Myiarchus gracilirostris Pelzeln, 1868, pp. 117, 183 (type locality, Villa Maria, Mato Grosso, Brazil; holotype in Vienna Museum, examined by Hellmayr).

Myiarchus tricolor Pelzeln, 1868, pp. 117, 182 (type locality, Rio de Janeiro and Sapitiba, Brazil; types in Vienna Museum, examined by Hellmayr).

Myiarchus coalei Ridgway, 1886, p. 520 (type locality, "Orinoco Valley"; holotype in National Museum of Natural History, examined).

Myiarchus tuberculifer tuberculifer: Berlepsch, 1907, p. 477 (new combination). Bangs and Penard,

1918, p. 79. Todd, 1922, p. 212 (in part; synonymy). Hellmayr, 1927, p. 180 (in part; synonymy). Zimmer, 1938a, p. 19.

Myiarchus tuberculifer tricolor: Berlepsch, 1907, p. 477 (new combination). Todd, 1922, p. 211 (synonymy). Hellmayr, 1927, p. 181 (synonymy). Zimmer, 1938a, p. 20.

Myiarchus tuberculifer clarus Zimmer, 1938a, p. 20 (type locality, Tapará, Rio Xingú, Brazil; holotype in the American Museum of Natural History, examined).

DIAGNOSIS: Back noticeably darker than in all other subspecies (table 7).

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 12): The most widespread of the five subspecies. Trinidad, southeastern Venezuela, and Colombia east of the Andes, southward through the Amazonian basin to the Yungas of Bolivia on the west and to Rio de Janeiro, Brazil, on the east. Follows the tributaries of the Amazon into the interior valleys of Peru. Absent from the more xeric regions of south-central and eastern Brazil. Tropical and subtropical zones, from near sea level to as high as 1600 m. Intergrades with *pallidus* in central and

eastern Venezuela, and with *atriceps* in the Yungas of Cochabamba, Bolivia.

Sympatric with *M. swainsoni* and *M. ferox*

throughout most of the range, less commonly with *M. tyrannulus*, which favors more xeric habitat. Possibly sympatric with *M. venezuelen-*

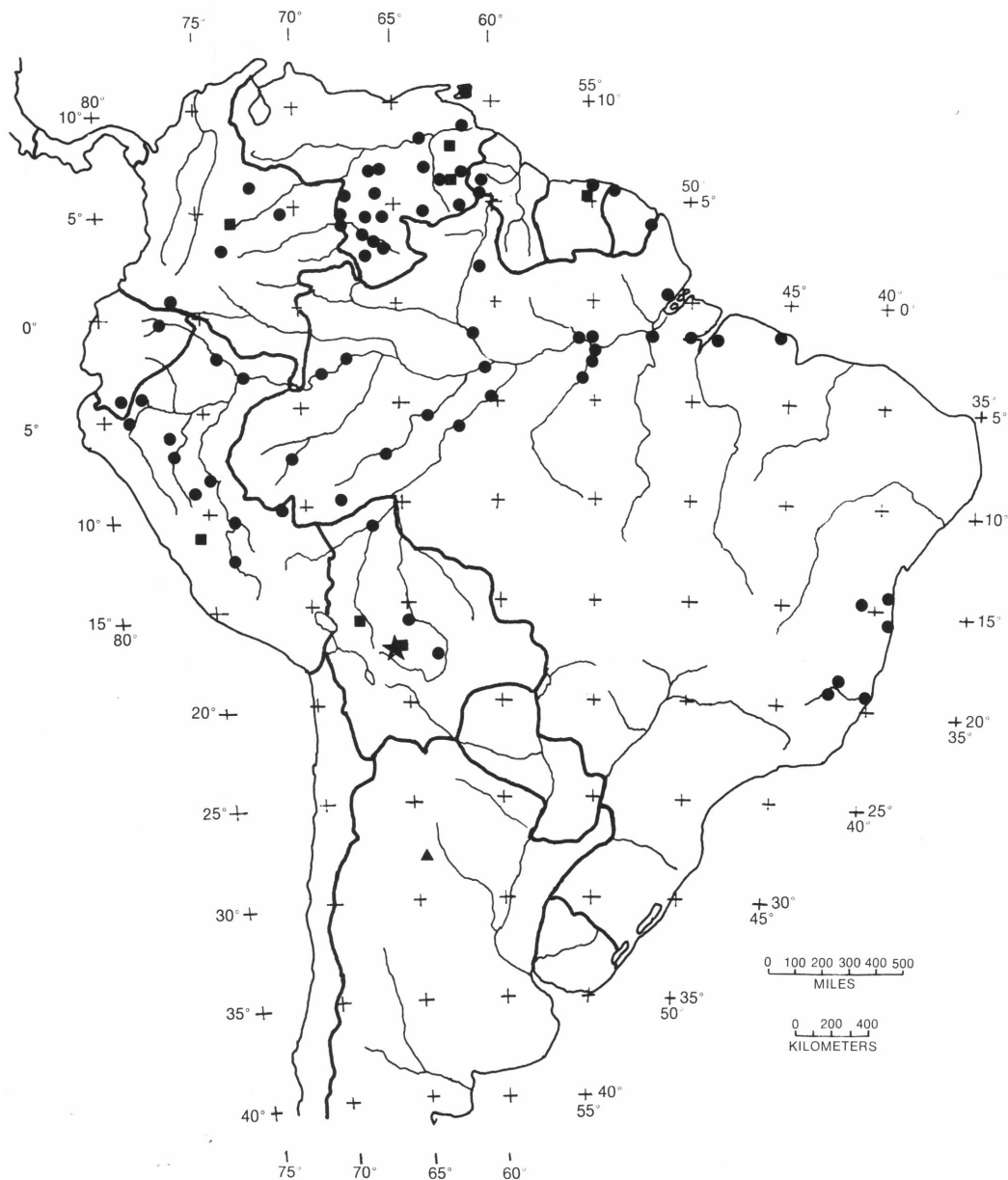


FIG. 12. Distribution of *Myiarchus tuberculifer tuberculifer* as indicated by the localities of specimens examined (circles) and of the sites where the author studied this taxon in the field (squares). The star marks an area of known intergradation between *M. t. tuberculifer* and *M. t. atriceps*. The triangle marks the locality of an extralimital specimen (p. 462). See page 462 for a list of these localities and page 458 for an itinerary of the author's fieldwork with this taxon.

sis in ecotonal habitat of northeastern Venezuela.

A specimen from Las Termes, Santiago del Estero, Argentina is the only record for that country where presumably the subspecies is no more than accidental (Olrog, 1949, p. 214). While in Tucumán, I had the opportunity to confirm the identity of this unique specimen. It is in late stages of prebasic molt, having been collected on November 16, 1929, and thus is on the molt schedule typical of nominate *tuberculifer* (rather than of *atriceps* of the higher elevations).

There are no specimens from Tobago. Herklots (1961) included Tobago in the range of *M. tuberculifer* on the basis of sight records and identifications by voice by Richard French. Subsequently I pointed out to French the great similarity between the whistled notes of *M. tuberculifer* and *M. venezuelensis*, a bird of the woodlands of the Main Ridge of Tobago, and he later accepted this explanation and dropped *M. tuberculifer* from his list of Tobago species (French, 1973).

Specimens examined, 215; localities, by country, from north to south and west to east (see fig. 12; asterisks denote author's study areas); TRINIDAD. VENEZUELA, Misión Araguaímujo, Delta Amacuro; Ciudad Bolívar, Bolívar; *El Palmar, Bolívar (Sierra de Imatata); Cerro El Negro, Bolívar; El Cambur, Bolívar; La Paragua, Bolívar; Carabobo, Bolívar; Cerro Auyan-tepui, Bolívar (Uaipán-tepui); *Kavanayén, Bolívar; Puerto Ayacucho, Amazonas (Caño Cataniapo); Cerro Yaví, Amazonas; Nericagua, Amazonas; Las Carmelitas, Amazonas; Cerro Parí, Amazonas; Sabana Kirichú, Bolívar; Cerro Paurai-tepui, Bolívar; San Fernando de Atabapo, Amazonas; San Antonio, Amazonas; El Merey, Amazonas; Boca del Río Ocamo, Amazonas; Caño Casiquiare, Amazonas. COLOMBIA, Palmar, Boyacá (Río Negro; La Colorada); Carimagua, Meta; *Villavicencio, Meta; Los Micos, Meta (Cordillera Macarena); Río Rumi-Yacu, Nariño (Río Churuyacu). GUYANA, Kamarang River (Paruima Mission); Mt. Roraima. SURINAM, Paramaribo (Lelydorp); *Phedra. FRENCH GUIANA, Mana; Pied Saut. BRAZIL, Serra

Grande, Rio Branco; Rio Tracajatuba, Amapá; Mirapenima, Amazonas; Faro, Pará (Lago Andirá); Obidos, Pará; Tapará, Pará; Benevides, Pará; Belém, Pará; Turiaçu, Maranhão; Santarém, Pará (Rio Tapajos, Igarapé Brabo, Igarapé Amorim); Tonantins, Amazonas; Caxiri-catuba, Pará; Manacapuru, Amazonas; São Paulo do Olivença, Amazonas; Itaituba, Pará (Villa Braga); Rozarinho, Amazonas (Igarapé Auará; Borba); Arimã, Amazonas; Marmellos, Amazonas; Santa Cruz, Amazonas; Hyutanahan, Amazonas; Nova Olinda, Acre; Ilheos, Baía; Boa Nova, Baía; Belmonte, Baía; Lower Suassuhy, Minas Gerais; Rio Doce, Minas Gerais (Rio Sacramento); Lagôa Juparanã, Espírito Santo (Rio Doce; Pao Gigante). ECUADOR, Limoncocha, Napo (Río Suno Abajo; San Jose Abajo); Guayaba, Loja. PERU, Boca Río Curaray, Loreto; Iquitos, Loreto (Puerto Indiana; Río Napo); Río Cenipa, Amazonas; San Ignacio, Cajamarca; Moyobamba, San Martín; El Tingo, San Martín; Yarinacocha, Loreto; Santa Elena, Huánuco; Balta, Loreto; Lagarto, Loreto; *San Ramón, Junín (Chanchamayo; Hacienda Mosela); Luisiana, Ayacucho. BOLIVIA, Riberalta, El Beni; *Yolosa, La Paz (Santa Ana); Boca Río Chaparé, Cochabamba; *Villa Tunari, Cochabamba (Todos Santos; Río Espíritu Santo; "Mission" San Antonio); *Yungas, Cochabamba; Buena Vista, Santa Cruz (Río Surutú; Santa Rita; Río Yapacani. ARGENTINA, Las Termas, Santiago del Estero.

REMARKS: In a form with as large a geographic range as in nominate *tuberculifer*, it is not unexpected to find some morphological variation. Historically, there have been attempts to use trinomials to designate subunits of this variable form. As indicated in the synonymy, I have chosen not to recognize some of these for, in my opinion, the differences evident in the material at hand are either inconsistent or at a level below that used for the formal recognition of subspecies in this study.

Hellmayr (1927) examined the types of two early names, *gracilirostris* from Mato Grosso, Brazil, and *tricolor* from Rio de Janeiro, Brazil. The former he considered "absolutely identical with Bolivian specimens" (topotypes of

TABLE 3
Wing Length (in Millimeters) in Samples of *Myiarchus tuberculifer*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. t. tuberculifer</i>					
Males	59	75 - 86	81.1 ± 0.36	2.75	3.39
Females	75	70 - 82	76.0 ± 0.33	2.89	3.81
<i>M. t. pallidus</i>					
Males	31	78 - 86	81.4 ± 0.36	2.03	2.49
Females	28	72 - 83	76.4 ± 0.51	2.69	3.51
<i>M. t. brunneiceps</i>					
Males	28	75 - 85	80.2 ± 0.52	2.74	3.41
Females	21	72 - 80	75.8 ± 0.47	2.14	2.82
<i>M. t. nigriceps</i>					
Males	27	75 - 84	80.5 ± 0.42	2.19	2.72
Females	22	73 - 81	76.0 ± 0.42	1.96	2.58
<i>M. t. atriceps</i>					
Males	60	82 - 95	89.4 ± 0.44	3.39	3.79
Females	47	77 - 90	84.2 ± 0.50	3.40	4.04
Intergrades between <i>tuberculifer</i> and <i>atriceps</i> ; Cochabamba, Bolivia, above 800 m.					
Males	23	79 - 93	85.8 ± 0.84	4.03	4.70
Females	12	76 - 91	82.6 ± 1.65	5.71	6.92
Combined Samples of <i>tuberculifer</i> , <i>pallidus</i> , <i>brunneiceps</i> , and <i>nigriceps</i>					
Males	145	75 - 86	80.9 ± 0.21	2.52	3.12
Females	146	70 - 83	76.0 ± 0.22	2.62	3.44

tuberculifer) and placed it in synonymy. He gave subspecific status to *tricolor*, following Todd (1922), but acknowledged that "single specimens are not always distinguishable from *M. t. tuberculifer*, and the race, as a whole, is not very satisfactory." Zimmer (1938a) recognized *tricolor*, but with considerable hesitancy, apparently, for he had written in unpublished notes in 1937, "these birds are very doubtfully separable from *tuberculifer* . . . the upper parts are identical." My spectrophotometric analysis confirms the lack of significant differences in the crown and back of samples of *tricolor* and *tuberculifer*. Where I have diagnosed subspecies of *M. tuberculifer* on the basis of coloration of the crown or back, the reflectance characteristics suggest a minimum overall color difference (DE) of at least 4.0 MacAdam units (tables 6 and 7). My sample of *tricolor*, though

admittedly small, shows no such difference in either crown (table 8) or back (table 9).

Zimmer and Phelps (1946) examined Ridgway's type of *coalei* from the "Orinoco" and placed it in synonymy with nominate *tuberculifer*. I have also examined this type and concur.

When Todd (1922) recognized *tricolor*, he did so on the basis of fresh material from the lower Amazon valley, not upon topotypical specimens from the vicinity of Rio de Janeiro. Zimmer (1938a) also noted apparent differences in the specimens from the lower Amazon, and he assigned the name *clarus* to a specimen from the Rio Xingú, in Pará, Brazil. Zimmer diagnosed *clarus* as having the crown "paler (less contrasting with the back)" and the "back rather brighter olive than in typical *tuberculifer*." My spectrophotometric analyses sug-

TABLE 4
Tail Length (in Millimeters) in Samples of *Myiarchus tuberculifer*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. t. tuberculifer</i>					
Males	62	66 - 79	72.7 ± 0.35	2.77	3.81
Females	72	61 - 76	68.1 ± 0.39	3.28	4.81
<i>M. t. pallidus</i>					
Males	29	71 - 78	74.3 ± 0.39	2.09	2.81
Females	29	64 - 75	69.5 ± 0.50	2.67	3.84
<i>M. t. brunneiceps</i>					
Males	27	68 - 81	72.3 ± 0.64	3.33	4.60
Females	20	64 - 73	68.2 ± 0.54	2.43	3.57
<i>M. t. nigriceps</i>					
Males	25	66 - 78	73.4 ± 0.64	3.18	4.32
Females	21	67 - 73	69.3 ± 0.39	1.80	2.59
<i>M. t. atriceps</i>					
Males	58	74 - 90	83.0 ± 0.47	3.55	4.28
Females	45	70 - 83	78.5 ± 0.45	2.99	3.81
Intergrades between <i>tuberculifer</i> and <i>atriceps</i> ; Cochabamba, Bolivia, above 800 m.					
Males	21	70 - 87	78.5 ± 1.03	4.71	6.00
Females	12	69 - 87	76.7 ± 1.91	6.61	8.62
Combined Samples of <i>tuberculifer</i> , <i>pallidus</i> , <i>brunneiceps</i> , and <i>nigriceps</i>					
Males	143	66 - 81	73.1 ± 0.24	2.90	3.97
Females	142	61 - 76	68.6 ± 0.24	2.91	4.25

TABLE 5
Body Weight (in Grams) in Samples of *Myiarchus tuberculifer*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Combined Samples of <i>tuberculifer</i> , <i>pallidus</i> , <i>brunneiceps</i> , <i>nigriceps</i>					
Males	20	18.0 - 24.0	21.0 ± 0.41	1.84	8.76
Females	17	14.2 - 23.0	19.0 ± 0.48	1.98	10.46
<i>M. t. atriceps</i>					
Males	21	16.4 - 25.0	22.0 ± 0.47	2.15	9.77
Females	21	18.0 - 27.0	21.8 ± 0.58	2.67	12.22

gest that there is no significant difference between the reflectance of the back in my sample of *clarus* and in my sample of nominate *tuberculifer* (table 9). The difference in reflectance of the crown of these samples (table 8) is at the very lowest level of difference in coloration between those subspecies that I am recognizing in this revision. My decision not to

recognize *clarus* is based principally on the comparatively small amount of differentiation in coloration from that of the nominate form, and also on the fact that Zimmer's type of *clarus* is not separable from many specimens of *pallidus*. I prefer to call attention to the fact that within the range of nominate *tuberculifer* there is a tendency for individuals in the lower

Amazon valley to differ slightly in crown color, in the same direction as exhibited by *pallidus* but to a lesser degree and over a smaller geographical area.

Myiarchus tuberculifer pallidus
Zimmer and Phelps

Myiarchus tuberculifer pallidus Zimmer and Phelps, 1946, p. 12 (type locality, Las Trincheras, Carabobo, Venezuela; holotype in the American Museum of Natural History, examined). Phelps and Phelps, 1963, p. 191. Meyer de Schauensee, 1964, p. 278.

DIAGNOSIS: Crown and back paler and crown browner than in all other subspecies (tables 6 and 7).

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 13): Northeastern Colombia and northern and western Venezuela. Tropical and subtropical zones, from sea level to 2000 m. Inter-

grades with *tuberculifer* in central and eastern Venezuela, and with *brunneiceps* in northern Colombia.

Sympatric with *M. ferox*, *M. panamensis*, and *M. venezuelensis* at lower elevations, and with *M. cephalotes* at higher elevations; less commonly sympatric with *M. tyrannulus*, which favors more xeric habitat.

Specimens examined, 132; localities, by country, from north to south and west to east (see fig. 13; asterisks denote author's study areas): COLOMBIA, Carraipía, Guajira; Santa Marta, Magdalena (Don Diego; La Tigra; Fundación; El Conejo; Cátagualito; Onaca; Las Nubes; Minca; Valparaíso); Fonseca, Guajira (Villaneuva; Cueva); Turbaco, Bolívar; Caracolicito, Magdalena; "Camp Costa Rica," Magdalena; Colosó, Sucre; Jaraquiel, Córdoba; Norosí, Bolívar; Ocaña, Norte de Santander; Villa Felisa, Norte de Santander; Bellavista, Norte de Santander; Río Sinú/Río Verde,

TABLE 6
Reflectance Characteristics of the Crown in Pairs of Samples of Adjacent Subspecies of
Myiarchus tuberculifer

Samples and Period of Collection	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>atriceps</i> (1894-1938)	58	3.41	0.46	Standard	
<i>nigriceps</i> (1897-1929)	17	3.26	0.60	-1.2	2.4
<i>nigriceps</i> (1897-1929)	17	3.26	0.60	Standard	
<i>brunneiceps</i> (1907-1915)	21	3.67	0.66	3.4	4.0
<i>brunneiceps</i> (1907-1915)	21	3.67	0.66	Standard	
<i>pallidus</i> (1874-1925)	58	4.39	0.92	5.4	6.8
<i>pallidus</i> (1874-1925)	58	4.39	0.92	Standard	
<i>tuberculifer</i> (1886-1946)	62	3.79	0.55	-4.0	4.2
<i>atriceps</i> (1894-1938)	58	3.41	0.46	Standard	
<i>tuberculifer</i> (1886-1946)	62	3.79	0.55	3.0	7.4

TABLE 7
 Reflectance Characteristics of the Back in Pairs of Samples of Adjacent Subspecies of
Myiarchus tuberculifer

Samples and Period of Collection	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>atriceps</i> (1894-1938)	59	7.85	0.81	Standard	
<i>nigriceps</i> (1897-1929)	17	7.34	0.52	-2.4	3.2
<i>nigriceps</i> (1897-1929)	17	7.34	0.52	Standard	
<i>brunneiceps</i> (1907-1915)	21	7.63	0.81	1.4	1.5
<i>brunneiceps</i> (1907-1915)	21	7.63	0.81	Standard	
<i>pallidus</i> (1874-1925)	57	8.17	0.86	2.6	3.5
<i>pallidus</i> (1874-1925)	57	8.17	0.86	Standard	
<i>tuberculifer</i> (1886-1946)	58	6.70	0.63	-6.8	6.8
<i>atriceps</i> (1894-1938)	59	7.85	0.81	Standard	
<i>tuberculifer</i> (1886-1946)	58	6.70	0.63	-5.4	5.5

TABLE 8
 Reflectance Characteristics of the Crown of Samples of *Myiarchus tuberculifer*
 from the Amazon and Orinoco Drainages

Samples and Period of Collection	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>tuberculifer</i> (1886-1946)	62	3.79	0.55	Standard	
"tricolor" (1928-1929)	4	3.76	0.11	-0.2	1.0
"clarus" (1930-1931)	8	4.26	0.61	3.4	3.9
<i>pallidus</i> (1874-1925)	58	4.39	0.92	4.4	4.7

Córdoba; La Palmita, Santander (El Cauca);
 Pavarandocito, Antioquia; Puerto Valdivia,
 Antioquia; Simití, Bolívar (Volador); Río

Cobugon, Boyacá; El Tambor, Santander (El
 Conchal); Segovia, Antioquia (Botero; Río
 Porce); Río Samaná, Caldas. VENEZUELA,

*Cerro El Cedro, Zulia; Cerro El Cerrón, Falcón; San Luis, Falcón; Chirgua, Yaracuy (Laguneta de Aroa); *Rancho Grande, Aragua (Cumbre de Turiamo; Ocumare de la Costa; Las Trincheras, Cumbre de Valencia, and Sierra de Carabobo, Carabobo); El Limón, Distrito Federal (Loma Redonda; Los Caracas; Colonia Tovar); Santa Lucía, Miranda; Cumaná, Sucre (Latal; Río Neverí; Los Altos; Cumanacoa); Quebrada Bonita, Sucre (San Antonio); El Guácharo, Sucre (Quebrada Seca; La Tigrera; Los Dos Ríos; Valle de Santa Ana; Valle de Campo Alegre; Caripe; Cerro Turumiquire); Yaguaraparo, Sucre; Cristóbal Colón, Sucre; La Sabana, Zulia (La Sierra); Motatán, Trujillo (Guamito); *Cubíro, Lara (Guarico; Anzoátequi); Encontrados, Zulia; El Vigía, Mérida (Azulita; Santa Elena); Mérida, Mérida; *Barinas, Barinas (La Veguita); Seboruco, Táchira; *San Fernando de Apure, Apure; Caicara, Bolívar (Quiribana de Caicara); Bramón, Táchira (Delicias); La Victoria, Apure.

REMARKS: In an early stage of this study, it occurred to me that the population to which Zimmer had assigned the name *pallidus* might be nothing more than an intermediate stage in a clinal gradient of plumage coloration between nominate *tuberculifer* of the Amazon basin and *brunneiceps* on the other side of the Andes. If this were the case, I was prepared to drop the use of a formal name (as I have done in my treatment of *M. swainsoni* "*amazonus*"; see p. 534) and simply describe the nature of the cline. After conducting an analysis of plumage

reflectance, however, it became clear that *pallidus*, though occupying a geographical position

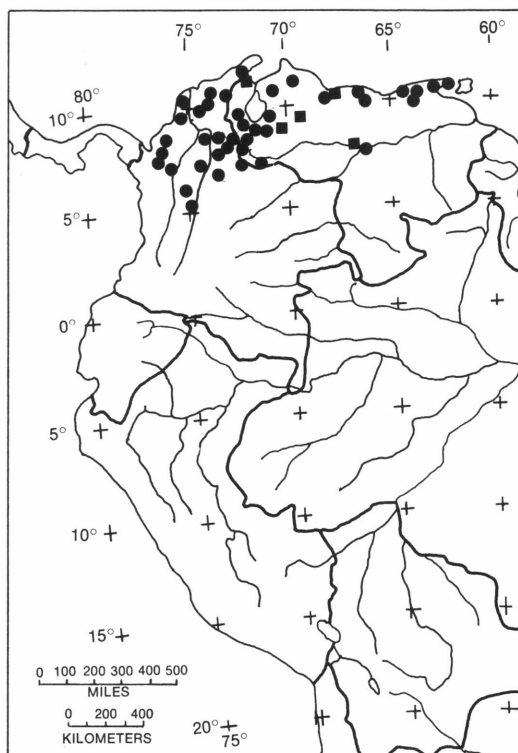


FIG. 13. Distribution of *Myiarchus tuberculifer pallidus* as indicated by the localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). See page 465 for a list of these localities and page 458 for an itinerary of author's field work with this taxon.

TABLE 9
Reflectance Characteristics of the Back of Samples of *Myiarchus tuberculifer*
from the Amazon and Orinoco Drainages

Samples and Period of Collection	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>tuberculifer</i> (1886-1946)	58	6.70	0.63	Standard	
"tricolor" (1928-1929)	4	6.89	0.53	1.0	1.2
"clarus" (1930-1931)	6	7.02	0.47	1.7	1.7
<i>pallidus</i> (1874-1925)	57	8.17	0.86	7.6	7.7

between *brunneiceps* and *tuberculifer*, did not occupy an intermediate position morphologically. The crown and back of *pallidus* are significantly paler in coloration than in either *tuberculifer* or *brunneiceps*, and the crown is browner than in either of those forms (tables 6 and 7).

Myiarchus tuberculifer brunneiceps Lawrence

Myiarchus brunneiceps Lawrence, 1861, p. 327 (type locality, Lion Hill, Panama Railroad; holotype in the American Museum of Natural History, examined).

Myiarchus nigriceps: Sclater and Salvin, 1864, p. 360. Ridgway, 1907, p. 650.

Myiarchus tuberculifer nigriceps: Chapman, 1917, p. 477. Bangs and Barbour, 1922, p. 219. Todd, 1922, p. 216 (in part). Hellmayr, 1927, p. 182 (in part).

Myiarchus tuberculifer brunneiceps: Hellmayr, 1927, p. 183 (new combination; synonymy). Zimmer, 1938a, p. 24. Meyer de Schauensee, 1964, p. 278.

DIAGNOSIS: Crown paler and browner than in *atriceps* and *nigriceps*, but not so pale or as brown as in *pallidus*. Back paler and greener than in *tuberculifer*. See tables 6, 7, and 12.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 14): From the Canal Zone of Panama south through the Cauca and Magdalena valleys of western Colombia to the Departments of Valle and Huila. Tropical and subtropical zones, up to 1500 m. Intergrades with the extralimital *bangsi* in western Panama, with *pallidus* in northeastern Colombia, and with *nigriceps* in southwestern Colombia.

Sympatric with *M. panamensis* over much of its range; possibly locally sympatric with *M. apicalis* and *M. cephalotes* in the Cauca valley.

Meyer de Schauensee (1950, 1964) assigned specimens from the Magdalena valley to nominate *tuberculifer*, but with some hesitancy. Zimmer (1938a) regarded birds from Andalucia, on the western slope of the Eastern Andes, upper Magdalena valley, as closer to *brunneiceps*. I concur with Zimmer, for the crowns of these birds are too dark for *tuberculifer*. I have seen two specimens taken by Carriker in the lower Magdalena valley and these are best assigned to *brunneiceps* as well. Nominate *tu-*

berculifer would appear to be restricted to the region east of the Andes in Colombia.

Specimens examined, 67; localities, by country, from north to south and west to east (see fig. 14; asterisk denotes author's study area): PANAMA, El Uracillo, Coclé; *Cerro Azul, Panamá (Canal Zone); Mandinga, San Blas; Chimán, Panamá; Chepigana, Darién; Tacarcuna, Darién (Río Armila, San Blas); Cisturo, Darién (Cerro Pierre; Boca Río Paya; Pucro); Río Piña, Darién (Río Jaqué). COLOMBIA, Nicoclí, Antioquia (Acandí, and Unguía, Chocó); Juradó, Chocó; Murindó, Antioquia; Dabeiba, Antioquia (Alto Bonito); Río Jurubidá, Chocó; Juntas, Chocó; Salento, Caldas (La Selva); Córdoba, Valle; Cali, Valle (San José; Yumbo; Río Frío); La Candela, Huila; Andalucia, Huila.

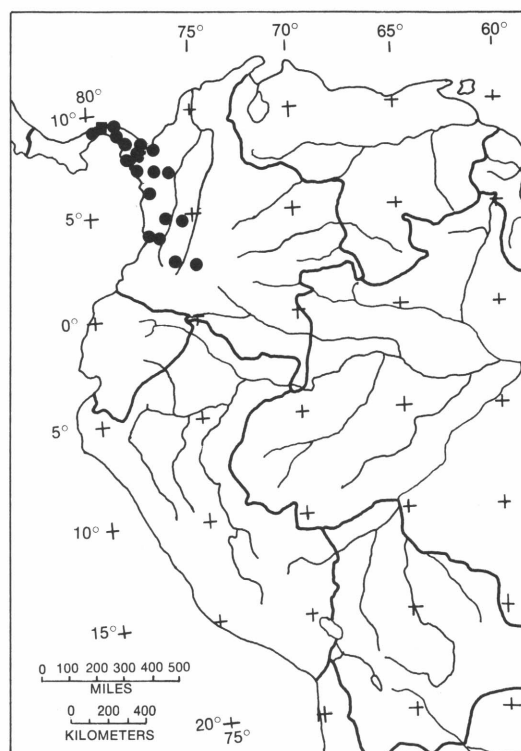


FIG. 14. Distribution of *Myiarchus tuberculifer brunneiceps* as indicated by localities of specimens examined (circles) and of site where author studied this taxon in the field (square). See page 468 for a list of these localities and page 458 for an itinerary of author's field work with this taxon.

Myiarchus tuberculifer nigriceps Sclater

Myiarchus nigriceps Sclater, 1860a, p. 68 (type locality, Pallatanga, Ecuador; holotype in the British Museum [Nat. Hist.]). Berlepsch, 1907, p. 477.

Myiarchus tuberculifer nigriceps: Hellmayr and von Seilern, 1912, p. 85 (new combination). Todd, 1922, p. 216 (in part; synonymy). Chapman, 1926, p. 528 (in part). Hellmayr, 1927, p. 182 (synonymy). Zimmer, 1938a, p. 24 (in part).

DIAGNOSIS: Crown as in *atriceps*, but noticeably blacker than in other subspecies. Separable from *atriceps* by its smaller size. See tables 3, 4, 6, 7, and 12.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 15): Upper Cauca valley of southwestern Colombia southward through Ecuador, west of the Andes, to the Departments of Guayas and Chimborazo. Tropical and subtropical zones, from sea level to 2400 m. Intergrades with *brunneiceps* in the upper Cauca valley of Colombia, and with *atriceps* in southern Ecuador.

Sympatric with *M. apicalis* in the upper Cauca valley of Colombia, with *M. cephalotes* at higher elevations throughout its range, and with *M. phaeocephalus* along the Pacific coast of Ecuador.

There has been some confusion in the literature as to the identity of the populations of *M. tuberculifer* in southwestern Colombia. Meyer de Schauensee (1950) assigned specimens from Popayán, in the upper Cauca valley, to *brunneiceps*. However, Miller (1963) believed that his specimens from Popayán were closer to *nigriceps*. I collected a series from the same locality and concur that they are not separable from specimens of *nigriceps* from Ecuador. A series from the region of Cali, somewhat farther north in the Cauca valley, is better assigned to *brunneiceps*, as has been suggested by Meyer de Schauensee (1950), Zimmer (1938a), and others.

Zimmer (1938a) had difficulty in determining the southern limits of the range of *nigriceps*, as this form is separable from *atriceps* to the south only by its smaller size. Purely as a matter of convenience, Zimmer designated the Ecuadorian/Peruvian border as the dividing line between the ranges of the two

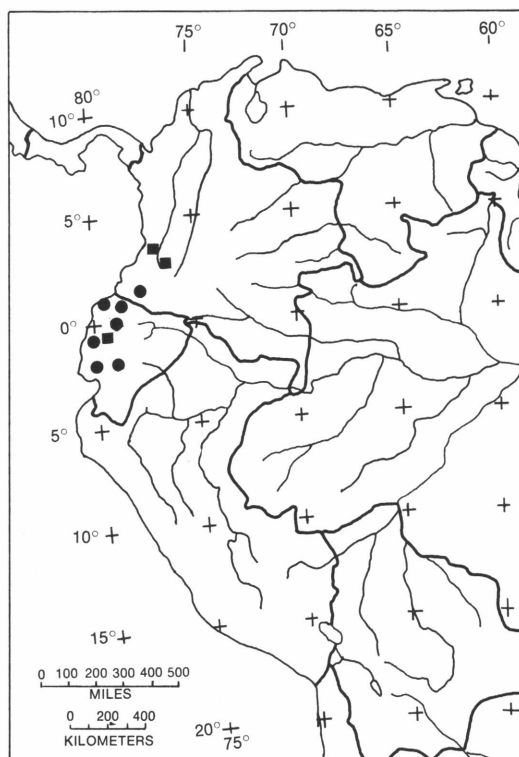


FIG. 15. Distribution of *Myiarchus tuberculifer nigriceps* as indicated by localities of specimens examined (circles) and of the sites where author studied this taxon in the field (squares). See page 470 for a list of these localities and page 458 for an itinerary of author's field work with this taxon.

forms. A more satisfactory boundary between *nigriceps* and *atriceps*, in my opinion, can be drawn in southern Ecuador at latitude 3° S, where the Andes are but a few kilometers from the Pacific Ocean (see frontispiece in Chapman, 1926). At this point there is a remarkable narrowing of suitable habitat for *M. tuberculifer*, i.e., humid tropical and subtropical woodlands, due to the impingement of the temperate zone of the Andes upon the arid tropical zone of the coast, thereby restricting gene flow between populations to the north and to the south of this narrow corridor. With the boundary drawn at latitude 3° S the subspecific range of variation in mensural characters for both *nigriceps* and *atriceps* is consistent with that observed in other subspecies of *M. tuberculifer* (tables 3 and 4).

Specimens examined, 63; localities, by country, from north to south and west to east (see fig. 15; asterisks denote author's study areas): COLOMBIA, *Queremal, Valle (Río Anchicayá; Río Raposo); *Popayán, Cauca (El Tambo; El Timbío; La Capilla; Río Munchique); Ricaurte, Nariño. ECUADOR, Esmeraldas, Esmeraldas; Intac, Imbabura (Paramba); Gualea, Pichincha; *Río Palenque, Pichincha (Santo Domingo; San Nicolas); Chone, Manabí; Chongón, Guayas; Pallatanga, Chimborazo (Chimbo; Coco; Pagma "Forest"; "Junction" Río Chanchan and Río Chiguancay; Bucay, Guayas).

Myiarchus tuberculifer atriceps Cabanis

Myiarchus atriceps Cabanis, 1883, p. 215 (type locality, San Xavier, Tucumán, Argentina; holotype in the Berlin Museum). Berlepsch, 1907, p. 477. Todd, 1922, p. 209 (synonymy).

Myiarchus tuberculifer atriceps: Hellmayr, 1920, p. 59 (new combination). Hellmayr, 1927, p. 182 (synonymy). Zimmer, 1938a, p. 22. Bond and Meyer de Schauensee, 1942, p. 346. Olrog, 1963, p. 257. Koepcke, 1970, p. 96.

DIAGNOSIS: Larger than other subspecies (see tables 3 and 4). Crown as in *nigriceps*, but noticeably blacker than in other subspecies (see tables 6 and 12). Vocal characters differ from other subspecies in having mean carrier frequency below 2.2 kHz. and as low as 1.7 kHz. in the Argentine populations.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 16): Southern Ecuador south through the Andes to the Province of Tucumán, Argentina. Subtropical and temperate zones; localities in Ecuador, Peru, and Bolivia range from 750 to 3400 m. and in Argentina from 700 to 1500 m. Intergrades with *nigriceps* in southern Ecuador and with *tuberculifer* in the Yungas of Bolivia (p. 482); parapatric with *tuberculifer* in the lower subtropical zone of Ecuador and Peru (p. 478).

Sympatric with *M. cephalotes* in Ecuador, Peru, and Bolivia. It is not clear to what extent even the southernmost populations of *atriceps* are migratory. Meyer de Schauensee's statement (1966) that "southern breeders migrate northward" was probably based on a similar statement in Olrog (1963). However, Argentine

specimens taken in Tucumán in April, and in Jujuy in July and August (austral winter) are evidence that at least some individuals do not migrate.

Specimens examined, 157; localities, by country, from north to south and west to east (see fig. 16; asterisks denote author's study areas): ECUADOR, Zaruma, El Oro (Portovelo); Celica, Loja (Cruzpamba; Guachanamá; San Bartolo); *Cajanuma Divide, Loja (Zamora; Zamora Chinchipe; Sabanilla; Gonzanamá). PERU, San Ignacio, Cajamarca; Palambra, Piura; Jaén, Cajamarca (Loma Santa; Tamborapa); Chachapoyas, Amazonas (Coroscha; La Lejia); *Abra de Porcula, Piura (San Felipe, Cajamarca); Leimebamba, Amazonas; Taulis, Cajamarca (Puente Mondaca); Cajamarca, Cajamarca; Cajabamba, Cajamarca (Pataz; Hacienda Limón; Hacienda Sunchubamba; Hacienda Huacrachuco; Hacienda Llaugueda, La Libertad); Samne, La Libertad (Soquián); Santa Clara, Ancash; *Chinchao, Huánuco (Acomayo); Huánuco, Huánuco (Huachipa, Huánuco); Alto Río Yurinaqui, Pasco; Obrajillo, Lima; Chelpes, Junín (Arequimamarca); Cordillera Vilcabamba, Cuzco (Yuraccyacu, Ayacucho); Torontoy, Cuzco; Marcapata, Cuzco; Cordillera de Carabaya, Puno; Oconeque, Puno (Santo Domingo; Inca Mine). BOLIVIA, *Yungas, Cochabamba; *Pojo, Cochabamba (Comarapa, Santa Cruz); Samaipata, Santa Cruz; Mizque, Cochabamba; Tomina, Chuquisaca; Monteagudo, Chuquisaca (Padilla; Río Azuero); 72 km. SE of Monteagudo, Chuquisaca; *Entre Ríos, Tarija; 80 km. S of Tarija, Tarija (118 km. S of Tarija). ARGENTINA, Orán, Salta (Santa María); Sierra de Santa Bárbara, Jujuy (Ledesma); San Pedro de Colalao, Tucumán; *Tucumán, Tucumán (Tafi Viejo; Tafi del Valle).

RELATIONSHIP OF
atriceps WITH *Myiarchus tuberculifer*

The differences in size and plumage coloration between *atriceps* and populations of *M. tuberculifer* throughout the Amazon and Orinoco basins are appreciable and of a larger magnitude than the differences between many of the species in this genus. Todd (1922) was one of the proponents for a separate specific

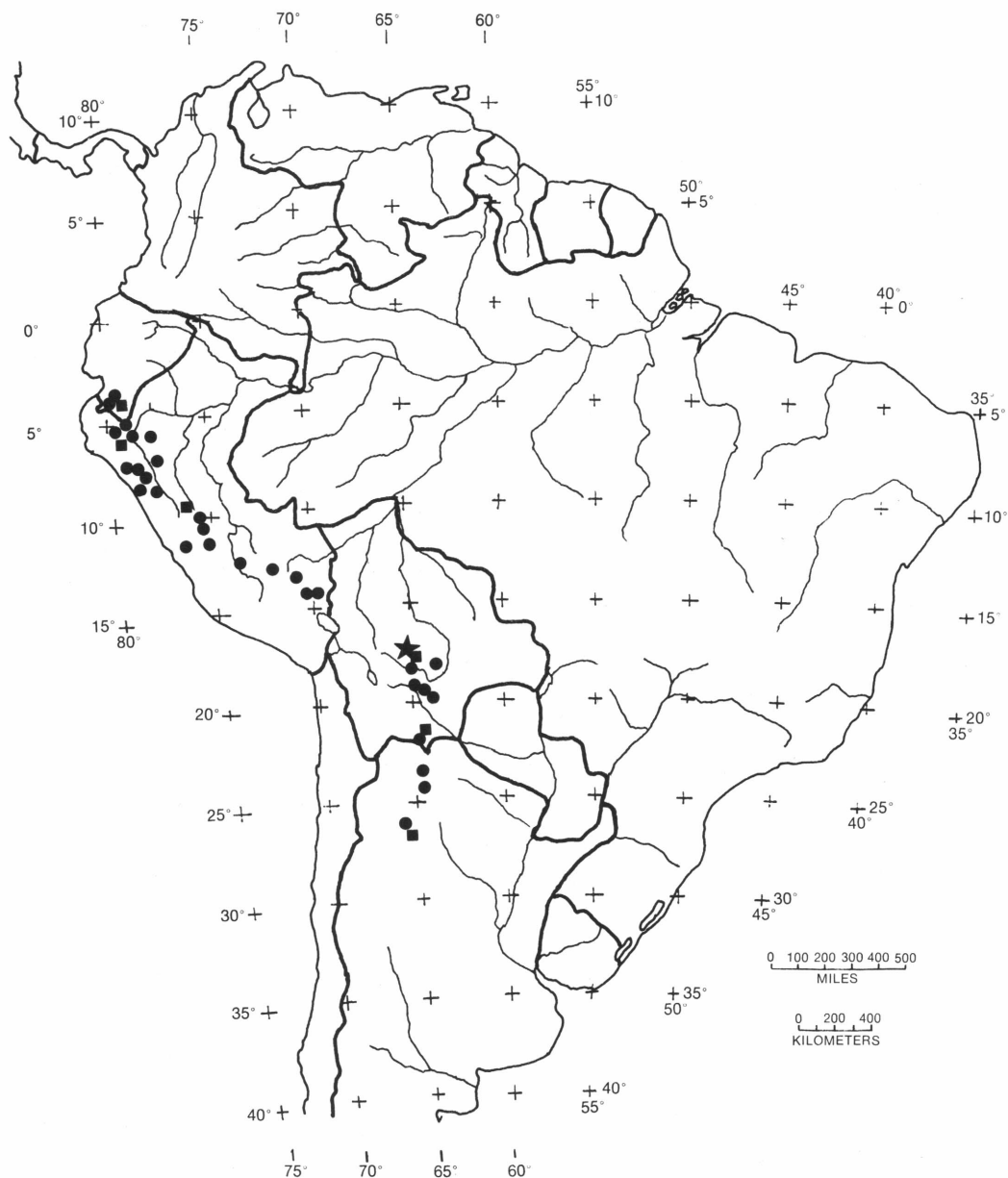


FIG. 16. Distribution of *Myiarchus tuberculifer atriceps* as indicated by localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). Star marks an area of known intergradation between *M. t. atriceps* and *M. t. tuberculifer*. See page 470 for a list of these localities and page 458 for an itinerary of author's field work with this taxon.

status for *atriceps*: "Mr. Hellmayr has lately proposed to make *atriceps* and *tuberculifer* conspecific, but after an extended comparison of

specimens we are satisfied that this arrangement does not correctly represent their real relationships. *M. atriceps* appears to be a Subtropical

Zone species, probably taking the place of *tuberculifer* at the higher altitudes, with absolutely no indication of intergradation." T aylor, in reviewing *Myiarchus* for a forthcoming volume of Peters's Check-list, wrote (personal commun.): "The status of *atriceps* will be a tough nut to crack and I find myself vacillating between subspecies and species. I shall have to possess my soul in patience until you have finished your field work . . . I am afraid that this is a situation where museum skins alone have little more to offer."

The relationship of *atriceps* to the various forms of *M. tuberculifer* did indeed prove to be one of the most challenging problems that I encountered in this revision.

INTERPRETATION AND SIGNIFICANCE OF PLAYBACK EXPERIMENTS

Since my South American fieldwork commenced in Argentina, my first experience with any South American population of *M. tuberculifer* was with *atriceps*. Available to me for purposes of locating territorial pairs and for playback experimentation were tapes that I had made of populations of *M. tuberculifer* in Middle America. Though working at localities where I had been assured by Claes Olrog (Instituto Miguel Lillo in Tucumán) that I would find *atriceps*, I had no luck in locating pairs with my Middle American tape. Six hours of fieldwork over a three-day period ended in failure. It was through the serendipitous playback of a tape of *M. swainsoni ferocior*, not of *M. tuberculifer*, that I located my first pair of *atriceps*. Subsequently I became aware, through playback experiments, that I could expect a low-level response from *atriceps* to the playback of *ferocior* (due to the great similarity in the frequency of the whistles of these two forms). When I had sufficient recordings of *atriceps* to prepare an Argentine *atriceps* playback tape, I had no difficulty in locating pairs of *atriceps* even at localities that had been previously unproductive when only Middle American *M. tuberculifer* tape had been used.

This lack of responsiveness on the part of *atriceps* to the casual use of Middle American *M. tuberculifer* tape in my reconnoitering for territorial pairs was confirmed in a more objec-

tive manner in a series of playback experiments with two pairs of *atriceps* near Tucumán in 1967. These birds were territorial and at the onset of breeding, judging from gonad condition. Both pairs were very responsive to Argentine *atriceps*, only slightly responsive to the repertoire of *M. swainsoni ferocior*, and not at all responsive to the playback tapes of Middle American *M. tuberculifer* or of seven other species of *Myiarchus* (*nugator*, *tyrannulus*, *antillarum*, *validus*, *oberi*, *crinitus*, and *stolidus*). The following field notes, made on November 13, 1967, illustrate the discriminatory ability of these *atriceps*:

Experiment 19—study area five, at 1350 m., on ridge just W of Tucumán. Tapes used, *M. swainsoni ferocior* vs. *M. nugator*. Pair calling from outside experimental area at start of experiment. Start at 10:21 A.M. Still calling out of area at 10:25. At 10:27, moved to within 30 feet of *ferocior* model, calling. Cable switch at 10:29, at which time the pair moved down the slope, just out of experimental area, still calling. Both birds calling about 50 ft. from the new *ferocior* model at 10:32. Same at 10:34, and at end of experiment. Possible low level response to *ferocior*, but not sustained.

Experiment 20—same locality, pair, and date as above. Tapes used, *atriceps* (Tucumán) vs. *M. tyrannulus*. Pair calling just outside experimental area at start at 10:38 A.M. Moved to midpoint in 30 seconds, calling well; to within 40 ft. of *atriceps* model by 10:41; to 20 ft. by 10:44; to 15 ft., in a "study"; to 10 ft., by cable switch at 10:45. Both birds reoriented at once, and moved to within 20 ft. of new *atriceps* model by 10:48. Moved back out to 40 ft. from *atriceps* model at 10:49. Out to 50 ft. at 10:50. Calling well at 35 ft. from *atriceps* model at end of experiment. Good, positive response to tape made from local population; no response to *tyrannulus*.

Experiment 21—same locality, pair, and date as above. Tapes used, *M. tuberculifer* (Middle America) vs. *M. antillarum*. Pair calling from outside experimental area at start at 11:51 (about 1 hour after termination of previous experiment). No response at all. Birds ceased calling by the time of cable switch. Location of birds unknown. Experiment discontinued after cable switch.

Experiment 22—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. *M. validus*. Location of pair unknown at start at 12:01 P.M. First heard *atriceps* at 12:04, high up slope above

experimental area. Pair moved down to 50 ft. from *atriceps* model at 12:07. Following cable switch, both birds moved over to new *atriceps* by 12:09, calling well. In "study" at 20 ft. at 12:10. At 12:12, both birds calling well in crown of tree above *atriceps* model, 30 ft. up. One moved down to 3 ft. from model at 12:14. Both within 10 ft. of *atriceps* model at 12:15 and end of experiment. Good, positive response to tape made from local population; no response to *validus*.

Experiment 23—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. *M. tuberculifer* (Middle America). Pair silent, location unknown at start at 12:20 P.M. First heard *atriceps* at 12:25, up the slope, outside experimental area. By 12:26, both were perched 20 ft. from *tuberculifer* model, then both crossed clearing at midpoint, to 30 ft. above *atriceps* model, calling excitedly. Cable switch at 12:28. Both moved back across clearing at 12:29, to 30 ft. from new *atriceps* model; then to 15 ft., calling well. Crisscrossing, 20 ft. from *atriceps* model. Calling well right up to end of experiment. Good, positive response to tape made from local population; capable of discriminating between Argentine *atriceps* and *M. tuberculifer* (Middle America), with only weak, if any, response to the latter.

The lack of responsiveness of Argentine *atriceps* to my Middle American *M. tuberculifer* tape prompted me to question whether the same Argentine population would be as unresponsive to the repertoire of other South American populations of *M. tuberculifer*. As a result of fieldwork in 1968 and 1969 I was able to put together a playback tape of the repertoire of Venezuelan *M. tuberculifer* (both *pallidus* and *tuberculifer*). In 1970 I returned to Tucumán and conducted a series of 19 experiments with four pairs of *atriceps*. The localities of most of these experiments were the same as those in 1967, but the birds were new, since the territorial birds involved in the 1967 studies had been collected. One pair was not responsive at all, but the other three were consistently very responsive to Argentine *atriceps*, unresponsive to the repertoire of *M. tuberculifer* (Venezuela), and of three other species of *Myiarchus* (*ferox*, *cephalotes*, and *swainsoni*). The following field notes, made on November 30, 1970, typify the discriminatory ability of these *atriceps*:

Experiment 33—study area four, on ridge just W of

Tucumán. Tapes used, *M. tuberculifer* (Venezuela) vs. *M. swainsoni* (Brazil). Can hear whistles of *atriceps* from outside the experimental area at start, 5:40 P.M. Bird continued to give whistles well up the slope above experimental area up through time of cable switch at 5:47. No response during second half of experiment.

Experiment 34—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. *M. cephalotes*. No birds calling prior to experiment; location of pair unknown. Start at 5:55 P.M. First heard calling up the slope at 5:57. One bird came to within 40 ft. of *atriceps* model at 5:59; to 25 ft. at 5:59:30, calling well. Second bird appeared at 50 ft. out from *atriceps* model. Cable switch at 6:02. One bird to midpoint by 6:04. Good, sustained vocal response. One in "study" at 6 in. from new *atriceps* model at 6:06. Pass at model from 6 in. away. Both birds in *atriceps* area at end of experiment. Good, positive response and reorientation to *atriceps*, following lack of response to *M. tuberculifer* (Venezuela) in previous experiment.

Experiment 35—same locality, pair, and date as above. Tapes used, *M. tuberculifer* (Venezuela) vs. Argentine *atriceps*. No birds calling, location unknown at start at 6:16 P.M. One bird showed high above *tuberculifer* area at 6:19, and over to *atriceps* area at 6:19:30, calling about 50 ft. above model. Over to midpoint at 6:20. Both birds at midpoint, calling excitedly. One dropped to low perch, 50 ft. from *atriceps* model. Both birds within 25 ft. radius of *atriceps* model. One to 6 ft. from model at 6:23. Both within 6 ft. of *atriceps* model at cable switch at 6:23. Both dropped back from new *tuberculifer* model in 30 seconds. One to midpoint by 6:25. Both at midpoint at 6:25:30. Both over new *atriceps* model at 6:26, about 30 ft. up, calling well. One to 20 ft. of *atriceps* model at 6:29. Calling well in *atriceps* area at end of experiment. Good, positive response and reorientation to Argentine *atriceps*, and lack of response to *M. tuberculifer* (Venezuela).

I was convinced of this ability of Argentine *atriceps* to discriminate between their own repertoire and that of Venezuelan and Middle American *M. tuberculifer*. They responded to the playback of Venezuelan and Middle American *M. tuberculifer* in the same manner as to the playback of other species in the genus, i.e., with little or no response. What of the reciprocal situation? Does nominate *tuberculifer* discriminate between its own repertoire and that of Argentine *atriceps*?

Subsequently, I had ample opportunity to

locate pairs of nominate *tuberculifer* in Venezuela, Surinam, and along the eastern slopes of the Andes in Colombia, Peru, and Bolivia, using reconnaissance tapes that I had made from recordings of Middle American and Venezuelan *M. tuberculifer*. I found that the Argentine *atriceps* tape was of no value for this purpose. My field notes on the behavior of a pair of nominate *tuberculifer* in Junín, Peru, illustrate this lack of response to Argentine *atriceps*, even though this particular pair had finished breeding and were undergoing prebasic molt on November 11, 1972:

Experiment 1—study area one, at 1050 m., near San Ramón, Junín, Peru. Tapes used, *M. ferox* vs. Argentine *atriceps*. Pair calling outside experimental area at start at 7:15 A.M. Still giving rolls outside area 7:17. At midpoint, 50 ft. out, at 7:19, giving hiccups and rolls. Still at midpoint at 7:20, giving occasional roll. Cable switch at 7:22, with birds still at midpoint and giving rolls and whee notes. Still at midpoint at 7:25, occasional roll. Birds silent by 7:27, location unknown. One roll from midpoint, at 7:28:30, about 75 feet out. Still there at end of experiment, giving very occasional call. No positive response!

Experiment 2—same locality, pair, and date as above. Tapes used, *M. tuberculifer* (Middle America) vs. *atriceps* (Argentina). Birds calling occasionally at midpoint just before start, at about 75 ft. out. Start at 7:33 A.M. Pair alerted at once, moved over to *tuberculifer* area, 50 feet up. 30 ft. from *tuberculifer* model at 7:35, calling vigorously. "Study" at 10 ft. from *tuberculifer* model. Both birds in a pass at 7:36, to a perch 30 ft. out, calling well. Another pass, within 2 ft. of *tuberculifer* model, at 7:37. Another pass, within 2 ft. Another pass within 3 ft. at 7:38. Another pass by both birds at 7:39, within 3 ft. of *tuberculifer* model. Another pass within 4 ft. Cable switch at 7:40. One to midpoint within 30 seconds. Both birds at midpoint by 7:41, calling. One to 30 ft. from new *tuberculifer* model at 7:43. To 10 ft., both calling well. One in to 5 ft. Both within 6 ft. Pass at 7:45. Both in pass, 3 ft. from *tuberculifer* model. Calling vigorously. Out to 30 ft. Out to 50 ft. Back in to 20 ft., then a pass at *tuberculifer* model at 7:47. Both still in *tuberculifer* area at end of experiment. Good, positive response to Middle American *tuberculifer*; capable of discriminating between Middle American *M. tuberculifer* and Argentine *atriceps*, with no response to the latter.

The lack of response of this pair of nomi-

nate *tuberculifer* in Peru was to take on added significance later, when I had completed an analysis of geographical variation in vocalizations and determined an altitudinal effect on body size and on mean frequency of vocalizations. I will return to this point later (p. 476).

With Argentine *atriceps* and nominate *tuberculifer* behaving toward each other's vocal repertoire in the manner of distinct species, and given the marked morphological differences between these two forms, I was anxious to determine how the subtropical populations farther north in the Andes would react to these two repertoires. Working with *nigriceps* near Popayán, Colombia, I found that I could locate and stimulate territorial pairs with either Middle American or Venezuelan *M. tuberculifer* tapes and that the tape of Argentine *atriceps* was ineffective for this purpose. Playback experiments confirmed this ability to discriminate between the tapes of Middle American *M. tuberculifer* and of Argentine *atriceps*. The following field notes, made on March 11, 1973, illustrate this differential response of a pair of *nigriceps* at the onset of breeding:

Experiment 17—at 4 km. study area, 1850 m. Tapes used, Argentine *atriceps* vs. *M. venezuelensis*. Experimental area included tree from which dawn song was delivered by the male earlier this morning. Birds silent at start, location unknown. Start at 7:33 A.M. Both showed, calling well, about 50 ft. above *venezuelensis* model at 7:34:30. Both still calling well in top of dead oak, 50 ft. above *venezuelensis* model at 7:37. No orientation to *atriceps* at all. Both still calling high up in canopy at the cable switch at 7:40. Moved over to midpoint at 7:42, still calling. 50 ft. above *venezuelensis* model at 7:43, giving rasping notes and hiccups. Both calling up the slope, about 100 ft. from the new *venezuelensis* model at 7:45. Remained high up on the slope until end of experiment. Very low level response, if any; no clear orientation toward *atriceps*.

Experiment 18—same locality, pair, and date as above. Tapes used, *M. tuberculifer* (Venezuela) vs. *M. panamensis*. Birds silent, location unknown at start at 7:56 A.M. Within 30 seconds, one began calling excitedly up the slope, above experimental area. Both high over *tuberculifer* model at 7:57, calling well. Crisscrossing high over *tuberculifer* area at 7:58. Both flew up the slope, out of area at 8:00. Back over *tuberculifer* model by 8:01. Closest approach to model has been about 50 ft. Calling well

at 8:02. Back up slope, still calling, at cable switch. One made a pass at new *panamensis* model at 8:04. Both reoriented to new *tuberculifer* model by 8:04:30. Dropping down to 40 ft. from model, calling well. Calling well about 30 ft. from model at 8:06. Calling about 80 ft. up the slope from *tuberculifer* model at 8:09. Back into *tuberculifer* area by end of experiment. Fairly strong response to Venezuelan *M. tuberculifer*.

I have discussed the geographical variation in the vocal characters of the *M. tuberculifer* complex (p. 457) and pointed out that the only variable among populations, including Argentine *atriceps*, is in the carrier frequency. The vocalizations of Argentine *atriceps* differ from

those of nominate *tuberculifer* only in their lower range of frequencies, but this difference is pronounced and readily apparent to the human ear. Presumably a discriminating response in playback experiments is dependent upon these differences in mean frequency.

There is a strong negative correlation between this variation in mean frequency of vocalizations and body size throughout the *M. tuberculifer* complex. An analysis of this regression of body size on frequency of vocalizations, illustrated in figure 17, helps to interpret the kinds of response that I found in my playback experiments. The vocalizations of *nigriceps*, for example, are at frequencies similar to

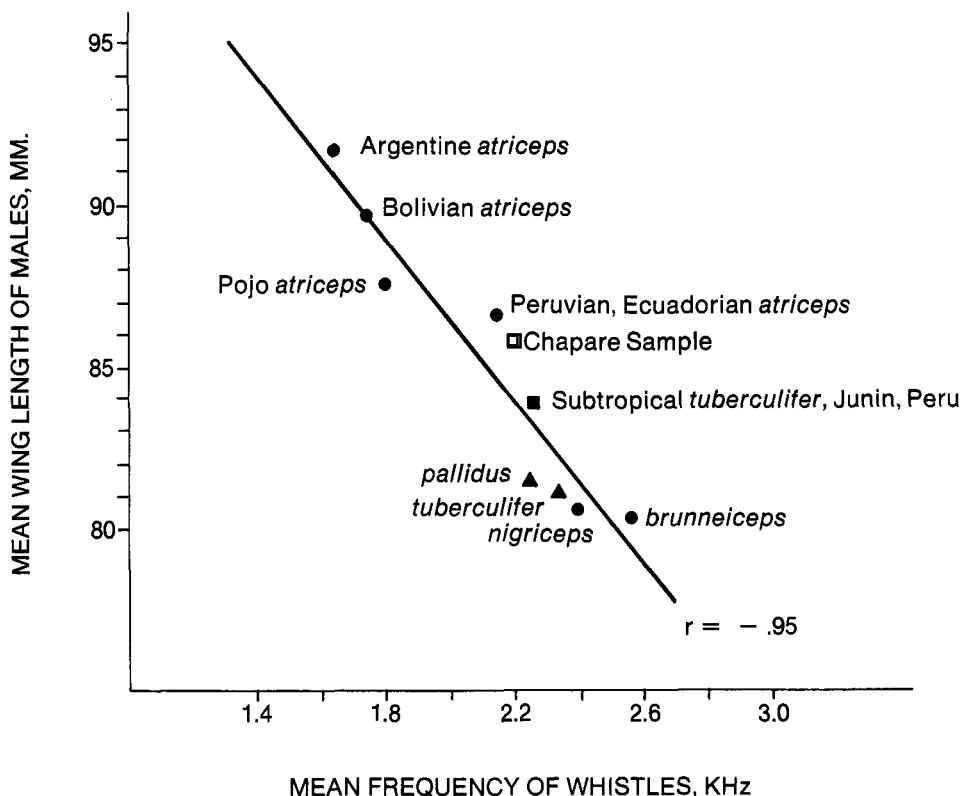


FIG. 17. Inverse correlation of body size (mean wing length in males) and frequency of vocalizations (mean frequency of whistles) in *Myiarchus tuberculifer*. Solid circles represent samples along the Andean cline of *atriceps*, *nigriceps*, and *brunneiceps*; solid triangles represent samples primarily of the Amazonian and Orinocan basins (*pallidus* and *tuberculifer*); solid square represents a sample of *tuberculifer* from subtropical zone of Junín, Peru, and illustrates an altitudinal effect on body size and frequency of vocalizations; open square represents a sample intermediate between *atriceps* and *tuberculifer*, from the Chapare, Department of Cochabamba, Bolivia. The correlation is significant at the 1 percent level.

those of *pallidus* and *tuberculifer*, and it is not surprising that the birds with which I worked near Popayán, Colombia, were responsive to playback of Venezuelan *tuberculifer* and showed little, if any, response to Argentine *atriceps*. My playback experiments with *atriceps* in northern Peru and southern Ecuador were disappointing, or so I thought at the time. Since I was unable to get any consistent response to either Venezuelan *M. tuberculifer* tape or to Argentine *atriceps* tape, I was unable to demonstrate any ability to discriminate between the two. Initially I attributed the poor level of response to the fact that all of my field work in northern Peru and southern Ecuador was at least two months prior to the breeding season for *atriceps* at those latitudes. In retrospect, it appears equally likely that the poor response of these particular birds could have been due to a real inability to discriminate, since their own vocalizations (not used in the playback experiments) are at frequencies intermediate between those that characterize Argentine *atriceps* and *tuberculifer* (fig. 17).

Critical field tests to determine how much of a change in frequency will alter responses in these playback experiments have not been done and were outside the scope of the present study. However, it is of interest that the subtropical population of *tuberculifer* with which I worked in Junín, Peru, have vocalizations at significantly lower frequencies (solid square in fig. 17) than the smaller-bodied populations of *M. tuberculifer* throughout northern South America and Middle America. Yet the Junín birds, even though they had finished breeding, were clearly responsive to playback of Middle American *M. tuberculifer* and showed no greater inclination than lowland populations to respond to Argentine *atriceps*.

With the use of this playback technique I have been able to demonstrate that the populations at the extreme ends of the clinal variation in mean frequency of vocalizations, i.e., those with the lowest carrier frequency and those with the highest carrier frequency, do not respond to the playback of each other's vocalizations. Under the simulated conditions of "sympatry" created by experimental playback, *atriceps* and nominate *tuberculifer* respond to

each other's vocal repertoire with the same indifference that they show to the vocalizations of other species within the genus. These findings suggest that if these forms were to come into contact and maintain these maximum differences in frequency of vocalizations, they would behave toward one another as congeners rather than as conspecifics.

But we have seen that there is a strong inverse correlation between mean frequency of vocalizations and body size. It can be demonstrated also that there is an altitudinal effect on body size in nominate *tuberculifer*, wherever the latter is found at higher elevations in the Andes. In Junín, Peru, for example, where I found no evidence of interbreeding, seven males of *tuberculifer* taken at elevations from 1050 to 1500 m. have a mean wing length of 83.9 mm. ($s_x = 0.46$), whereas 24 *tuberculifer* males from lower elevations at the western perimeter of the Amazon basin have a mean wing length of 79.9 mm. ($s_x = 0.51$). When nominate *tuberculifer* moves up the eastern slopes of the Andes, we can then predict that the populations at higher altitudes will consist of individuals of somewhat larger size and with vocalizations of somewhat lower frequencies. Consequently, the populations of *tuberculifer* most likely to come into contact with *atriceps* will have vocalizations approaching those of *atriceps* in frequency characteristics, and this phenomenon would be independent of whether or not there is interbreeding. Looking at this from another point of view, it is because of this altitudinal shift in frequency of vocalizations, which in effect minimizes the vocal differences between the two forms, that vocal characters may no longer operate as an effective barrier to interbreeding. A corollary of this is that intermediacy in frequency of vocalizations *per se* cannot be used as proof of interbreeding between *atriceps* and nominate *tuberculifer*.

PHYSICAL AND ECOLOGICAL BARRIERS AT THE NORTH END OF THE ANDEAN CLINE

The Andean cline of *atriceps*, *nigriceps*, and *brunneiceps* is an essentially continuous series of freely interbreeding populations from the temperate and subtropical zones of Argentina

north to the tropical zone of eastern Panama (fig. 4). There is nothing about the variation in mean frequency of vocalizations (fig. 17) or in body size (fig. 18) along this cline that suggests the operation of any physical or ecological barrier between populations, other than the reduced gene flow hypothesized for southern Ecuador as the basis for the logical demarcation between *atriceps* and *nigriceps* (p. 469). There is no gap in size between *atriceps* and *nigriceps* (fig. 18) as implied by Todd (1922), arguing for the specific status of *atriceps*. I have pointed out (p. 455) that the breeding cycles of the populations at the extreme ends of this cline are completely out of synchrony, but the shift from December to May breeding is a

gradual one, forming yet another cline in that regard.

The northern South American races (*brunneiceps* and *nigriceps*) of this complex are effectively isolated by the Andes from populations of nominate *tuberculifer* that occur along the western perimeter of the Amazon basin. The eastern range of the Colombian Andes provides an effective barrier between *brunneiceps* and *tuberculifer*, and I have seen no evidence that these forms come into contact. If they were to meet, however, one would predict interbreeding since their breeding cycles are similar and their vocalizations have the same frequency range. In northwestern Ecuador *nigriceps* occupies the tropical and lower sub-

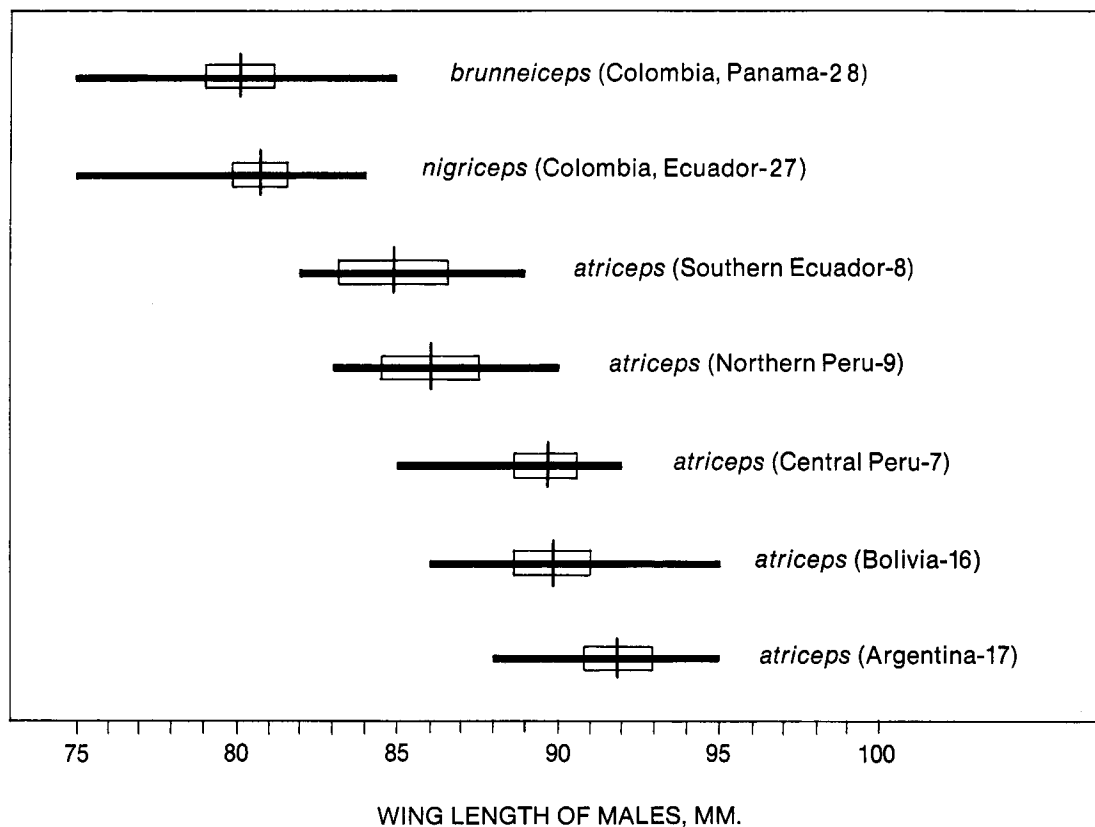


FIG. 18. Cline in body size (wing length of males) among samples of *atriceps*, *nigriceps*, and *brunneiceps*. Sample sizes are in parentheses. Horizontal bars represent range, means are indicated by vertical lines, and boxes indicate $\pm 2 \times$ the standard error of the mean.

tropical zones up to elevations of less than 2400 m., with no opportunity to cross over the Andes and come into contact with *tuberculifer*.

POTENTIAL CONTACT ZONE BETWEEN *atriceps* AND *tuberculifer*

There is no comparable physical or ecological barrier between *atriceps* and nominate *tuberculifer*. *Myiarchus tuberculifer atriceps* crosses the lower Andes in southern Ecuador and northern Peru and can be found in the subtropical zone of the headwaters of the Amazon. Nominate *tuberculifer* has been taken up to elevations of 1600 m. in the lower subtropical zone along the eastern fringe of the Andes and above the principal tributaries of the Amazon that drain the interior valleys of Peru. Consequently the two forms are in potential contact from southern Ecuador south through Peru and into Bolivia (fig. 4).

Because of the altitudinal effect upon body size and mean frequency of vocalizations, one must be cautious when looking for evidence of interbreeding throughout this zone of potential contact. Neither intermediacy in frequency of vocalizations nor in body size may be used as proof of interbreeding between lowland and highland populations, though such intermediacy can be expected as a consequence of interbreeding, if and when it occurs.

The crown of *atriceps* is noticeably blacker than the browner crown of nominate *tuberculifer* and the reflectance characteristics of the crown are of potential importance as an index to interbreeding between these forms. However, the use of this character is complicated

because crown color changes with time (undergoes "foxing") in museum specimens of both *atriceps* and *nigriceps*. The data substantiating this change with time are presented in table 10, where samples of both *atriceps* and *nigriceps* have been pooled, regardless of locality, and measured for crown reflectance characteristics according to period of collection. This change involves a noticeable paling, the crown becoming brighter and slightly browner in older museum specimens, and the degree of change is significant in specimens collected 30 or more years ago. I could not establish a comparable change with time in the crown color of museum specimens of nominate *tuberculifer* (table 11). The observed difference in crown color between these particular samples of *tuberculifer*, though probably not significant, cannot be ignored completely for it suggests a slight darkening of the crown of *tuberculifer* with time, i.e., a change in the direction of the crown color of *atriceps*. In critical determinations of interbreeding, comparisons of old specimens of *tuberculifer* and of *atriceps* should be avoided, in order to maximize the differences in crown color.

There is no evidence to support a relationship between altitude and crown color in this complex; therefore, reflectance characteristics of the crown can be used as an index to interbreeding between lowland and highland forms. The arguments against an altitudinal effect on crown color include the following:

1. The distribution of crown reflectance characteristics among the populations of *atriceps*, *nigriceps*, and *brunneiceps* is not clinal as it is with respect to body size and frequency

TABLE 10
Change with Time in Reflectance Characteristics of the Crown of Museum Specimens of
atriceps and *nigriceps*

Collection Period	N	Mean	S.D.	Brightness (Percent)		Color Difference (MacAdam Units)	
				t	P	DL	DE
1970-1974	44	3.12	0.44	—	—	Standard	
1950-1969	20	3.19	0.45	0.58	>.25	0.6	1.9
1930-1949	20	3.33	0.51	1.68	<.05	1.8	5.3
1910-1929	36	3.38	0.50	2.45	<.01	2.2	4.8
1890-1909	18	3.44	0.50	2.46	<.01	2.7	6.8

TABLE 11
Reflectance Characteristics of the Crown of Museum Specimens of Nominate *tuberculifer* from Colombia, Ecuador, Peru, and Bolivia According to Period of Collection

Collection Period	N	Mean	S.D.	Brightness (Percent)		Color Difference (MacAdam Units)	
				t	P	DL	DE
1961-1974	25	3.92	0.64	0.82	>.20	0.9	2.0
1920-1946	31	3.80	0.46	—	—	Standard	

of vocalizations (table 12). There is no significant difference in the crown color of *atriceps* and *nigriceps*, but there is a conspicuous difference between the crown colors of *nigriceps* and *brunneiceps* that is the basis for subspecific distinction.

2. There are no differences in the crown color of tropical lowland populations and subtropical highland populations of *nigriceps* in Ecuador. All *nigriceps* populations have black crowns though they may range in altitude from sea level to over 2000 m.

3. Crown reflectance among the other subspecies of *M. tuberculifer* is not correlated with altitude, and tropical lowland populations may be pale-crowned (*pallidus*) or darker-crowned (nominate *tuberculifer*).

4. A sample of *tuberculifer* from the lower subtropical zone of Junín, Peru (1050 to 1500 m.) does not differ significantly ($t = 0.78$, $P = >.4$), with respect to crown reflectance, from a sample of nominate *tuberculifer* from lower elevations along the western perimeter of the Amazon basin (table 13).

5. If we categorize specimens of nominate *tuberculifer* from the western perimeter of the Amazon basin (exclusive of the Department of Cochabamba, Bolivia) as to (1) those collected above 1000 m. and (2) those collected below 1000 m., we find no evidence of an altitudinal effect upon the reflectance characteristics of the crown (table 14).

One aspect that has not been discussed in the literature on the interrelationships between *atriceps* and *tuberculifer* is the timing of their respective breeding seasons. I have already pointed out that (p. 455) the breeding season for nominate *tuberculifer* along the eastern edge of the Andes in Ecuador, Peru, and Bolivia is

TABLE 12
Non-Clinal Variation in Reflectance Characteristics of the Crown in Samples of *atriceps*, *nigriceps*, and *brunneiceps*

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>atriceps</i>	107	3.26	0.48	Standard	
<i>nigriceps</i>	32	3.28	0.51	0.2	1.8
<i>brunneiceps</i>	24	3.75	0.71	4.0	7.9

from August to October. These same populations undergo a complete prebasic molt from October through March. The breeding season of *atriceps*, on the other hand, varies clinally. In southern Ecuador, *atriceps* breeds from March through June and undergoes a complete prebasic molt from July through October. The breeding cycles of the two forms are so completely out of phase at the northern end of the range of potential contact, that it is unlikely interbreeding would be possible. Farther south along the Andes *atriceps* breeds progressively earlier. In northern Peru the data suggest a breeding cycle from February through April, still well out of phase with that of *tuberculifer* at lower elevations. There are insufficient data to comment on southern Peru, but at the southern end of the cline in Bolivia and Argentina *atriceps* breed from mid-November through December. Even at the southern end of the range of potential contact, the breeding seasons of the two forms only barely approximate one another. On the basis of compatibility in reproductive cycles, then, it would be in Bolivia

TABLE 13
Similarity in Reflectance Characteristics of the Crown in Subtropical and Tropical Samples of
Nominate *tuberculifer*, Compared with *atriceps*

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>atriceps</i> from Peru (1953-1973)	7	3.03	0.36	Standard	
Subtropical <i>tuberculifer</i> from Junín, Peru (1972)	7	4.09	0.34	9.2	11.4
Tropical <i>tuberculifer</i> from Peru, Colombia, Ecuador, Bolivia (1961-1974)	17	3.86	0.74	7.2	13.5

TABLE 14
Lack of an Altitudinal Effect upon the
Reflectance Characteristics of the Crown in
Samples of Nominate *tuberculifer* from the
Western Perimeter of the Amazon Basin
(except Cochabamba, Bolivia)

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>tuberculifer</i> above 1000 m.	14	3.85	0.42	Standard	
<i>tuberculifer</i> below 1000 m.	42	3.85	0.58	0.0	1.9

that one might predict interbreeding between these zonal representatives, if it occurs at all.

It was Zimmer (1938a) who first called attention to possible intergradation between *atriceps* and *tuberculifer*. His evidence consisted of American Museum specimens from three localities along the zone of potential contact: (1) three specimens from Zamora Chinchipe, southeastern Ecuador; (2) one specimen from San Ignacio, Cajamarca, northern Peru, and (3) two specimens from Roquefalta, Cochabamba, Bolivia.

One of the Ecuadorian specimens (AMNH 167706) was taken at Guayaba (1340 m.) along the Upper Río Zamora, on November 20. Zimmer referred it to "*nigriceps*" (my *atriceps*), but acknowledged that the crown showed a trend toward *tuberculifer*. The crown, when

measured with the recording spectrophotometer, is paler and browner than the mean for a large sample of nominate *tuberculifer* from the western perimeter of the Amazon basin (table 15). The specimen is very worn, like other specimens of *tuberculifer* at that season (end of the breeding cycle), and quite unlike specimens of Ecuadorian *atriceps* that have completed their prebasic molt and are in fresh plumage in November. I have no hesitation to refer it to nominate *tuberculifer*.

A second Ecuadorian specimen (AMNH 129994) was taken at Zamora, also along the Upper Río Zamora, on October 17. Zamora is at the junction of the tropical and subtropical zones and is a region of potential contact of these forms. Although the printed altitude on the specimen label is 600 m., it is likely that the specimen was actually collected in the subtropical zone on the mountain slopes above the river (Chapman, 1926). In contrast to the Guayaba specimen, the Zamora bird is in fresh plumage, and the crown is as dark as a large sample of *atriceps* collected during an equivalent period (table 15). Todd (1922) and Chapman (1926) referred it to "*nigriceps*" (my *atriceps*). I submit that these two specimens (from Guayaba and Zamora) support the hypothesis that the two forms may actually overlap one another zonally in southern Ecuador, by virtue of their asynchronous breeding cycles. A third specimen from the Upper Río Zamora, taken at Sabanilla (1700 m.) on November 10 (AMNH 167703), could not be analyzed spectrophotometrically because of the

TABLE 15
Reflectance Characteristics of the Crown of Two Specimens from the Upper Río Zamora, Ecuador,
a Region of Potential Contact between *atriceps* and *tuberculifer*

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>atriceps</i> (1910-1929)	36	3.38	0.50	Standard	
AMNH 129994 (1913)	1	3.31	—	-0.6	2.7
AMNH 167706 (1920)	1	4.55	—	9.4	11.4
<i>tuberculifer</i> from western perimeter of the Amazonian basin (1920-1946)	31	3.80	0.46	3.4	6.9

condition of the crown plumage, but the plumage is fresh and I have no hesitancy in assigning it to *atriceps*.

Zimmer (1938a) believed that the trend in crown color toward that of *tuberculifer* was even more pronounced in a specimen (AMNH 181494) taken in the arid tropical zone of northern Peru, near San Ignacio, Cajamarca, on May 8, but he preferred to assign it to *atriceps*. Chapman (1926) considered it to be "fairly typical of *tuberculifer*." It is a female, with crown reflectance characteristics closer to those of *tuberculifer*. Mensural characteristics also argue for its assignment to *tuberculifer* (table 16; $t = 0.99$, $P = >0.3$). Zimmer apparently was unaware of a Carriker specimen (MCZ 179515) of *atriceps* also taken near San Ignacio (1200 m.) on August 1. It too is a female, but with crown reflectance characteristics closer to those of *atriceps*, and mensural characteristics also closer to those of *atriceps* (table 16; $t = 0.87$, $P = >0.4$). The plumage in these two specimens from San Ignacio are about in the same condition, i.e., only moderately worn, as one would predict on the basis of molt cycles. The female *tuberculifer* presumably finished its prebasic molt in March, hence a May specimen should show only moderate wear. The female *atriceps* presumably finished its prebasic molt in July and an August specimen would be only moderately worn. These two specimens from northern Peru lend further credence to the hypothesis that, in the northern part of the region of potential contact, *atriceps* and *tuberculifer* may occupy the same or contiguous zones

TABLE 16
Measurements (in Millimeters) of Two
Specimens from San Ignacio, Cajamarca, Peru,
A Region of Potential Contact between
atriceps and *tuberculifer*

Sample	N	Wing		Tail	
		Mean	S.D.	Mean	S.D.
<i>tuberculifer</i> ♀♀ from northern Peru	10	77.3	1.64	70.9	2.21
AMNH 181494, ♀	1	77	—	70	—
MCZ 179515, ♀	1	85	—	77	—
<i>atriceps</i> ♀♀ from northern Peru	7	82.9	2.27	77.1	1.57

without actually intergrading, due to the fact that their respective breeding cycles are out of phase.

One might look for signs of introgression resulting from interbreeding between *atriceps* and *tuberculifer* throughout this zone of potential contact. If we use the reflectance characteristics of the crown as an index to interbreeding, and categorize specimens of nominate *tuberculifer* from the western perimeter of the Amazon basin (exclusive of the Department of Cochabamba, Bolivia) as to (1) those collected within 200 km. of the range of *atriceps* and (2) those collected beyond 200 km. of the range of *atriceps*, we find no evidence of introgression (table 17). Specimens of *tuberculifer* taken nearest *atriceps* do not have crowns that are blacker (less brown) than specimens taken further from *atriceps*, as one might expect if there

TABLE 17
Lack of Introgression in Reflectance Characteristics of the Crown in Specimens of
Nominate *tuberculifer* Collected near the Range of *atriceps*

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>tuberculifer</i> within 200 km. of <i>atriceps</i>	35	4.00	0.64	1.6	1.9
<i>tuberculifer</i> beyond 200 km. of <i>atriceps</i>	16	3.79	0.62	Standard	

were introgression with respect to this character. In the samples available to me, the reverse was actually the case, i.e., the sample collected farthest from *atriceps* had the darker crowns, on average, though the difference is probably not significant ($t = 1.10$, $P = >0.2$).

INTERBREEDING IN THE YUNGAS OF BOLIVIA

The two specimens (AMNH 148612 and 148613) from Roquefalta, Bolivia, that impressed Zimmer (1938a) because of their relatively small size, were collected in the Bolivian Yungas, a term that has been used for the eastern slopes of the Andes in the Departments of La Paz and Cochabamba, a region of strongly dissected topography and one of transition from tropical lowlands to temperate highlands. These specimens, as well as much additional material taken subsequently, take on added significance in light of the earlier discussion of the timing of the respective breeding seasons of *atriceps* and *tuberculifer*, for it is in Bolivia that the reproductive cycles of the two forms are likely to be most compatible. Todd reexamined the Roquefalta specimens and additional material collected later by Franz Steinbach and, in a letter to Zimmer in 1951, also acknowledged the smaller size: "I am quite unable to find any characters wherewith to distinguish these Bolivian specimens from a series of *nigriceps* from Ecuador and Colombia, and would unhesitatingly refer them to that race. Incidentally, this conclusively disposes of the idea that *atriceps* and *tuberculifer* are conspecific—just as I contended long ago." Zimmer replied: "I am unable to agree with you. . . . I think it may be one of those cases

where an intermediate population bears a striking resemblance to a form living in a very distant region."

For an analysis of the interrelationship of *atriceps* and *tuberculifer* in this critical region of possible contact, I assembled a series of 32 specimens taken by Steinbach and Carriker in the Yungas of Cochabamba, as well as 53 specimens taken by Steinbach, Carriker, Crossin, and others from elsewhere in Bolivia. To these I contributed 16 specimens of my own, of known voice and breeding condition, collected during six weeks of fieldwork in Bolivia in October and November of 1974. All of the Bolivian specimens that show some degree of intermediacy were taken in the Department of Cochabamba, principally in the Province of Chapare.

Figure 19 illustrates the intermediacy in body size of those specimens taken in the Chapare above 800 m., compared with *atriceps* and nominate *tuberculifer* taken elsewhere in Bolivia. Both Todd (in correspondence with Zimmer) and Traylor (in correspondence with me) were puzzled by the fact that Steinbach, according to the specimen labels, took birds of two size classes from the same locality, Incachaca, and presumably during the breeding season. I visited Incachaca (3000 m.) in the hope of shedding some light on this problem, and spent the better part of two days playing reconnaissance tapes without attracting a single *Myiarchus*. I later had the opportunity to meet Franz Steinbach in Cochabamba and discuss with him the collection that he had made at Incachaca over a six-month period some 47 years earlier. The first point that I established was a confirmation of my suspicion that the

habitat at Incachaca had been altered drastically since 1927; this could account for my failure to find any *Myiarchus* there. I also established that his specimens labeled "Incachaca" were actually taken over a radius of many kilometers and a range of altitude of at least 1500 m. In the absence of detailed information on the exact geographical relationship between the specimens in question, I have chosen to pool all the specimens taken in the Chapare above 800 m. and treat them as the "Chapare sample." The histograms given for the Chapare sample in figure 19 argue against a bimodal distribution in body size and suggest the kind of intermediacy that one would expect if highland and lowland

populations were interbreeding freely. These data on body size cannot be used as proof of interbreeding, however, because of the correlation that has been established between altitude and body size.

The vocalizations of the four pairs of *M. tuberculifer* that I found at elevations of 825 to 1600 m. in the Chapare were analyzed critically with respect to mean frequencies and compared with the vocalizations I recorded from nominate *tuberculifer* and from *atriceps* at lower and higher altitudes, respectively, in Bolivia (fig. 20). These analyses were standardized by confining measurements to the highest frequencies represented in the whistle and roll, and in the

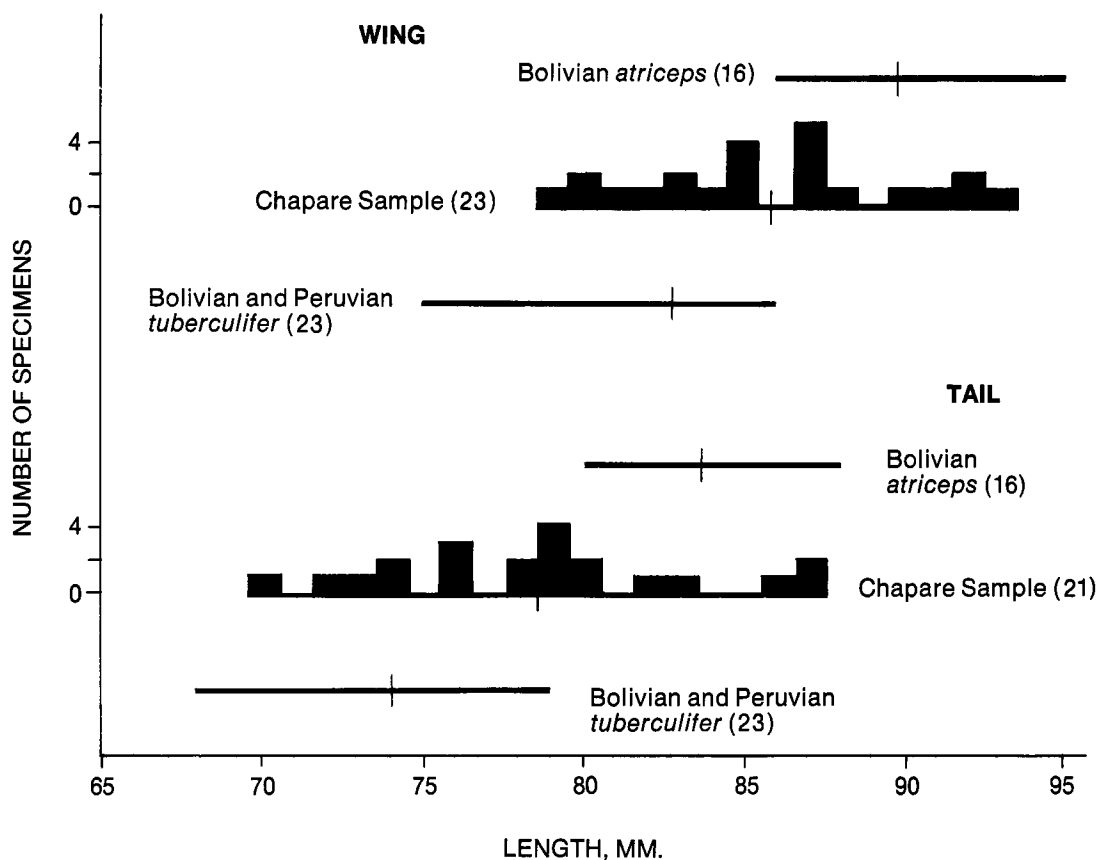


FIG. 19. Intermediacy in body size (wing and tail length, in mm.) of males of *Myiarchus tuberculifer* in the Chapare, Department of Cochabamba, Bolivia, from above 800 m. Sample of Bolivian *atriceps* was taken from localities south of Cochabamba. Sample sizes are in parentheses. Horizontal bars represent range, and means are indicated by vertical lines. Histograms are given for the Chapare sample to illustrate lack of a bimodal distribution.



FIG. 20. Intermediacy in frequency of vocalizations of *Myiarchus tuberculifer* in the Chapare, Department of Cochabamba, Bolivia. Chapare sample is from four pairs, 825 to 1600 m. Bolivian *tuberculifer* sample is from two pairs at 340 m. in the Department of Cochabamba. Bolivian *atriceps* sample is from four pairs in the Departments of Cochabamba and Tarija, at 2070 to 2500 m. Numbers of graphs analyzed are in parentheses. Horizontal bars represent range, and means are indicated by vertical lines. See text for procedure used in measuring frequency.

first element of the hiccup. Frequency scales were calibrated on the basis of the standard reference tone of known frequency that I routinely place on each tape at the time of the original recording. The intermediacy of the Chapare sample, with respect to frequency of vocalizations, could have been predicted on the basis of the intermediacy of this sample in terms of body size. Again, the results are consistent with the hypothesis that these birds interbreed in the Chapare, but do not constitute proof.

Table 18 indicates intermediacy of the Chapare sample with respect to the reflectance

characteristics of the back. Recently collected specimens had to be eliminated from this analysis for they have significantly greener and brighter backs. They apparently undergo a much more rapid change in reflectance characteristics of this portion of the plumage with time elapsed since collection. Consequently, my samples were inadequate to determine what effect, if any, altitude has on back coloration in nominate *tuberculifer*. Without this information, no significance can be attached to the intermediacy of the Chapare sample with respect to reflectance characteristics of the back. Here again, such intermediacy is to be ex-

pected, if in fact interbreeding occurs in this region.

The intermediacy in reflectance characteristics of the crown in the Chapare sample (table 19) does suggest interbreeding between lowland and highland forms, and takes on added significance when one realizes that the population of subtropical *tuberculifer* that I sampled in Junín, Peru, at an altitude comparable to that of the Chapare sample, did not differ significantly from lowland *tuberculifer* with respect to the crown (compare tables 13 and 19).

On the basis of data from populations to the north and south I had concluded that it would be in Bolivia where the reproductive cycles of nominate *tuberculifer* and *atriceps* are likely to be most compatible. Consequently, one of the primary objectives of my fieldwork in the Department of Cochabamba in 1974 was to determine the breeding condition of these birds along a transect from tropical lowlands through subtropical and temperate highlands. Table 20 presents the data acquired from this transect that indicate a shift in the breeding season with altitude in populations of *M. tuberculifer* in the Department of Cochabamba. My hypothesis is that no such shift occurs altitudinally farther

north in the zone of potential contact between *atriceps* and *tuberculifer*, due to the greater degree of asynchrony in breeding seasons between lowland and highland forms. The only data that I have for subtropical populations of nominate *tuberculifer* in Peru and Ecuador come from specimens that I collected in Junín, Peru, in mid-November, and they support this hypothesis. Three males and four females taken at altitudes from 1050 to 1500 m. had finished breeding and were well into the prebasic molt; i.e., they were on the same breeding schedule as *tuberculifer* in the tropical zone (August to October). Birds taken at comparable altitudes in mid-November in the Yungas of Bolivia were just commencing to breed and showed no indication of molt (table 20).

My interpretation of these data from the Chapare sample is that there is interbreeding between lowland *tuberculifer* and highland *atriceps*, and it is likely that interbreeding occurs in other portions of the Yungas of Bolivia as well. On the basis of previous discussions, there are two prerequisites for such interbreeding to occur: (1) the breeding seasons of lowland and highland populations must be reasonably compatible, and (2) the vocal differ-

TABLE 18
Reflectance Characteristics of the Back in the Chapare Sample, Compared with Samples of *atriceps* and *tuberculifer* from Elsewhere in Bolivia

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
Bolivian <i>tuberculifer</i> (1921-1938)	11	6.82	0.53	Standard	
Chapare Sample	32	7.30	0.55	2.4	2.5
Bolivian <i>atriceps</i> (1936-1938)	16	7.38	0.44	2.9	4.1

TABLE 19
Reflectance Characteristics of the Crown in the Chapare Sample, Compared with Samples of *atriceps* and *tuberculifer* from Elsewhere in Bolivia

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
Bolivian <i>atriceps</i> (1972-1974)	28	3.01	0.45	Standard	
Chapare Sample (1974)	7	3.42	0.64	3.5	6.0
Bolivian <i>tuberculifer</i> (1967-1974)	5	4.52	0.45	13.1	18.0

TABLE 20
Shift of Breeding Season with Altitude in Populations of *Myiarchus tuberculifer*
in the Department of Cochabamba, Bolivia

Altitude in Meters	Estimated Breeding Season	Specimen Data (gonad size in mm.)	Locality
340	August and September	AMNH 821936: Oct. 26, 1974, testes 4×2 , remige molt, heavy body molt	8 km. N of Villa Tunari, Chapare
		AMNH 821935: Oct. 26, 1974, testes 5×3 ; light body molt, no remige molt	10 km. N of Villa Tunari, Chapare
825	September and October	AMNH 821958: Oct. 25, 1974, testes 8×5 (post-breeding regression), no molt	42 km. SW of Villa Tunari, Chapare
		AMNH 821959: Oct. 25, 1974, ovary and oviduct not enlarged, no molt	
975	mid-October to mid-December	AMNH 821957: Nov. 19, 1974, ovary and oviduct slightly enlarged, brood patch beginning to develop, no molt	48 km. SW of Villa Tunari, Chapare
1500	mid-October to mid-December	AMNH 821961: Oct. 24, 1974, testes 11×6 , no molt	55 km. SW of Villa Tunari, Chapare
		AMNH 821960: Oct. 24, 1974, ovary and oviduct not enlarged, no molt	
1600	November and December	AMNH 821955: Nov. 18, 1974, testes 10×6 , no molt	70 km. SW of Villa Tunari, Chapare
		AMNH 821956: Nov. 18, 1974, ovary and oviduct slightly enlarged; brood patch beginning to develop, no molt	
2300	November and December	AMNH 821943: Oct. 31, 1974, testes 9×5 , no molt	37 km. E of Pojo, Carrasco
		AMNH 821944: Oct. 31, 1974, ovary and oviduct not enlarged, no molt	
2500	November and December	AMNH 821949: Nov. 17, 1974, testes 10×6 , no molt	38 km. E of Pojo, Carrasco
		AMNH 821948: Nov. 17, 1974, ova up to 3 mm., oviduct enlarged, no molt	

ences between the small-bodied lowland form and the larger-bodied highland form must be minimized so that differences in frequency no longer operate as an effective isolating mechanism. Both prerequisites appear to have been met in the Chapare. The best evidence for interbreeding lies in the intermediacy of the reflectance characteristics of the crown (table 19) and in the shift of breeding season with altitude (table 20), neither of which has been demonstrated for any other locality within the zone of possible contact. Further support for the concept of interbreeding comes from having established intermediacy in body size (and lack of a bimodal distribution in the geographically inter-

mediate population), mean frequency of vocalizations, and reflectance characteristics of the back. There is no evidence that denies interbreeding in the Chapare.

Let us return now to the use of playback experiments. While in Bolivia in 1974, I had the opportunity to conduct some experiments with two pairs of *atriceps* in the Department of Tarija, well south of the range of nominate *tuberculifer*. Both pairs were territorial and at the onset of breeding (as indicated by gonad condition). Their response was similar to that observed in experiments with Argentine *atriceps* a number of years earlier, i.e., positive to playback of Argentine *atriceps* and negative

to the repertoire of Venezuelan and Middle American *M. tuberculifer*. The following field notes, made on November 9, 1974, illustrate the discriminatory ability of the Tarija birds:

Experiment 17—study area two, at 2100 m., 35 km. NW of Entre Ríos. Tapes used, Venezuelan *M. tuberculifer* vs. nominate *swainsoni* (Brazil). Pair silent, location unknown at start at 11:21 A.M. No response at all, before or after cable switch.

Experiment 18—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. *cephalotes*. Location of pair still unknown. Start at 11:36. One bird showed in 30 seconds, at *cephalotes* end of experimental area. Moved to midpoint by 11:38. Both birds at midpoint, calling well. In to 40 ft. of *atriceps* model. In to 30 ft. by 11:40. To 10 ft. above *atriceps* model, calling well. In a "study" at 10 ft., other bird out at 15 ft. from *atriceps* model. At the cable switch, I substituted Venezuelan *tuberculifer* for *cephalotes*. Both birds had drifted over to old *cephalotes* (new *tuberculifer*) area by the time the second half of the experiment began at 11:47. Within one minute, both birds had reoriented to the new *atriceps* area (flew right through the *tuberculifer* area to get to new *atriceps*). In a "study" at 8 ft. from *atriceps* model, calling well. 5 ft. at 11:49. Cross-over by both birds. Out to 30 ft., both calling excitedly. Both within 15 ft. of *atriceps* model, calling well. Crossover at 11:52. Another crossover at 11:53. Still near *atriceps* model at end of experiment. Strong response to *atriceps*; no response to *tuberculifer*.

In the Chapare, however, the responses to playback were more equivocal. A pair that had recently bred, but not yet molting, were tested on October 25, 1974:

Experiment 5—study area one, at 825 m., 42 km. N of Villa Tunari. Tapes used, *ferox* vs. Middle American *M. tuberculifer*. Birds calling up the slope at start at 6:48 A.M. Two birds appeared at midpoint within one minute. In to 40 ft. of *tuberculifer* model by 6:50. In to 20 ft. In to 8 ft. of *tuberculifer* model. In "study" at 1 ft., at 6:51. One at 1 ft., one at 3 ft., both calling well. Crisscrossing. Both about 3 ft. from *tuberculifer* model, calling well. Both back to midpoint at 6:53. Stayed out at 40 ft. for three minutes. One back to 10 ft., then to 4 ft. of *tuberculifer* model at cable switch. Lost interest in old *tuberculifer* area; moved out to edge of experimental area. To midpoint by 6:58. One to 40 ft. of new *tuberculifer* at 7:00, but lost interest and moved up the slope. Only a fair response to *tuberculifer*.

Experiment 6—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. *cephalotes*. Birds calling up the slope, out of experimental area, at start at 7:10 A.M. Calling picked up, but remained up the slope. One bird at midpoint. Both within 30 ft. of *atriceps* model at 7:12. One in to 15 ft. at 7:13. Crisscrossing of *atriceps* area. Both in "study" at 8 ft. of *atriceps* model. Calling well within 10 to 15 ft. radius of *atriceps*. Both out to 40 ft. at 7:15, and there at cable switch, calling well. To midpoint within 30 seconds. Both still at midpoint at 7:19. Both to 40 ft. of new *atriceps* model by 7:20, still calling excitedly. In to 30 ft. by 7:21. Back out to 50 ft. by 7:22, and there at end of experiment. Fair response to *atriceps*.

Experiment 7—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. Middle American *tuberculifer*. Birds silent at start, location unknown. Start at 7:30 A.M. Both birds appeared, calling well, within 30 seconds, in to 40 ft. of *tuberculifer* model. Both within 8 ft. of *tuberculifer* model at 7:33. Both sitting 6 ft. above model, calling well. Jays have found us, and are scolding loudly. The pair lost interest and moved back up the slope. Only a fair response to *tuberculifer*.

Another pair of Chapare birds, at the onset of breeding on November 19, had been very responsive to and had actually been located by a reconnaissance tape made from recordings of *nigriceps* in Colombia. Ten minutes later I began experimentation:

Experiment 19—study area two, at 975 m., 48 km. SW of Villa Tunari. Tapes used, Argentine *atriceps* vs. *ferox*. Birds silent at start, location unknown. Start at 12:02 P.M. No response at all during entire 14 minutes of playback (in an area that had attracted the pair at once with *nigriceps* reconnaissance tape). I held up the *atriceps* speaker and broadcast the repertoire in all directions, to no avail. At 12:15, one bird gave a whistle just outside the experimental area, but easily within hearing distance of the playback. No approach.

Experiment 20—same locality, pair, and date as above. Tapes used, Argentine *atriceps* vs. tape made from recording of Pojo *atriceps* (at 2500 m., 37 km. E of Pojo in the SE corner of the Department of Cochabamba). Birds calling several hundred feet away at start at 12:25 P.M. Both birds entered Pojo *atriceps* area within 30 seconds, calling well. Both there within 30 ft. at 12:28. To 20 ft., calling excitedly, at 12:29. In to 10 ft. of Pojo *atriceps* model at 12:30. Back out to 20 ft. Complete disregard for

Argentine *atriceps* area! To midpoint 30 seconds after cable switch. In to 30 ft. by 12:34, still calling well. Both within 30 ft. of new Pojo *atriceps* model, calling well, at 12:35. In to 15 ft. at 12:36. Still there, calling well, at end of experiment.

There are several significant points in the response of this pair of Chapare birds at 975 m. I discovered, quite fortuitously, that the birds reacted strongly to playback of *nigriceps*, but not to Argentine *atriceps*. This can be explained by the closer similarity of the mean frequency of vocalizations of the Chapare birds to that of *nigriceps* than to Argentine *atriceps*. The subsequent clear discrimination between tapes of Argentine *atriceps* and of Pojo *atriceps*, and strong response to the latter, suggests a closer similarity of the vocalizations of the Chapare birds to those of Pojo *atriceps* than to Argentine *atriceps*. These similarities in frequency characteristics are confirmed in figure 17. A third pair of Chapare birds, breeding at 1600 m., was located too far from my vehicle to permit use of the standardized dual speaker experiment. By alternating playback from two tape recorders I was able to establish good response to Venezuelan *M. tuberculifer* and to playback of Pojo *atriceps*. Often the pair could be attracted to within 4 m. of the recorder, and the birds were quite vocal in response to both of these tapes. In contrast, I could not elicit any consistent response to playback of Argentine *atriceps*. In retrospect, I am reminded of the similar negative response to playback of Argentine *atriceps* that I observed in a subtropical population of nominate *tuberculifer* in

Junín, Peru. The Junín sample and the Chapare sample are characterized by similar body size and mean frequency of vocalizations (fig. 17). The responses to playback that I observed in the Chapare are consistent with the hypothesis that these birds are intergrades between the lowland and highland populations.

The transition, morphologically and vocally, from nominate *tuberculifer* in the tropical lowlands to *atriceps* in the subtropical and temperate highlands takes place altitudinally over a horizontal distance of less than 100 km. in the Chapare. We have already seen that a similar transition occurs, though over a much greater distance horizontally, along the south-to-north cline of Andean populations of this complex. With respect to body size and mean frequency of vocalizations, the population along the Andean cline that might be considered "equivalent" to the Chapare sample would be one involved in effecting the transition from *atriceps* to *nigriceps* in southern Ecuador (fig. 17). With respect to reflectance characteristics of the crown, the "equivalent" population would be one involved in the transition from *nigriceps* to *brunneiceps* in southern Colombia (tables 6 and 12). This comparison of vertical and horizontal clines brings to mind the exchange of correspondence between Todd and Zimmer cited earlier in this section (p. 482), in which Todd admitted difficulty in distinguishing the Chapare birds from *nigriceps* in Ecuador and Colombia, and Zimmer's very perceptive suggestion that the resemblance might be fortuitous.

MYIARCHUS VENEZUELENSIS LAWRENCE

This monotypic South American endemic is restricted to the island of Tobago and a rather narrow zone of northern Colombia and Venezuela (fig. 26). Curiously, it is not well represented in museum collections. The species is nonmigratory.

The form *venezuelensis* has heretofore been considered by most workers to be a geographical representative of *M. ferox*, along with *insulicola* of Tobago and *panamensis* of Colombia, Panama, and Costa Rica. In the present study *venezuelensis* has been found to be speci-

fically distinct from and sympatric with both *M. ferox* and *M. panamensis*, and *insulicola* is placed in synonymy with *M. venezuelensis*.

DIAGNOSIS: Outer pair of rectrices with outer vanes noticeably paler than inner vanes, and external margins of rectrices other than outer pair conspicuously fringed with Antique Brown. (Caution: paler external margin or brownish fringe may be lost with strong feather wear.) Other than this fringing of the external margins, rectrices of adults not conspicuously marked with Antique Brown. In fresh speci-

mens, entire mandible black (no seasonal or geographical variation; but paling occurs, rendering the character unreliable in older museum specimens; see fig. 21) and color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics includes repeated rasp-whistles and "wheer-r-r" notes, but *no* rolls or "huit" notes. Dawn song consists solely of plaintive whistles (*no* "huit" notes) rendered at intervals of several seconds.

HABITAT (FIGS. 22-23): Tropical zone. Clearings in and borders of rather dry deciduous woodlands, and in cocoa plantations (Aragua). Clearings in forested areas of the higher portions of Tobago, not the coastal lowlands.

BREEDING AND ANNUAL CYCLE: I found no nest of this species and I know of no reference in the literature. Presumably it is a cavity nester and uses nesting materials similar to those of its congeners.

The breeding season includes the months of April and May, and possibly March and June. Males taken in May had testes measuring up to 12 by 6 mm., whereas specimens in January have testes as small as 3 by 2 mm. Most females taken in May exhibit brood patches, and two females taken on May 1 had eggs in much enlarged oviducts. I have an observation of a recently fledged juvenile being fed by adults in Zulia, Venezuela, on May 15.

The prebasic molt may begin as early as late May, and most specimens taken from late July through October are molting their remiges. I have seen two specimens in juvenal plumage: one taken in Carabobo, Venezuela, on July 20, and one taken in Lara, Venezuela, on July 24.

VOCAL CHARACTERS: The analysis of vocal characters of *M. venezuelensis* is based on recordings from these samples: Zulia, Venezuela, one pair; Yaracuy, Venezuela, one pair; Ara-

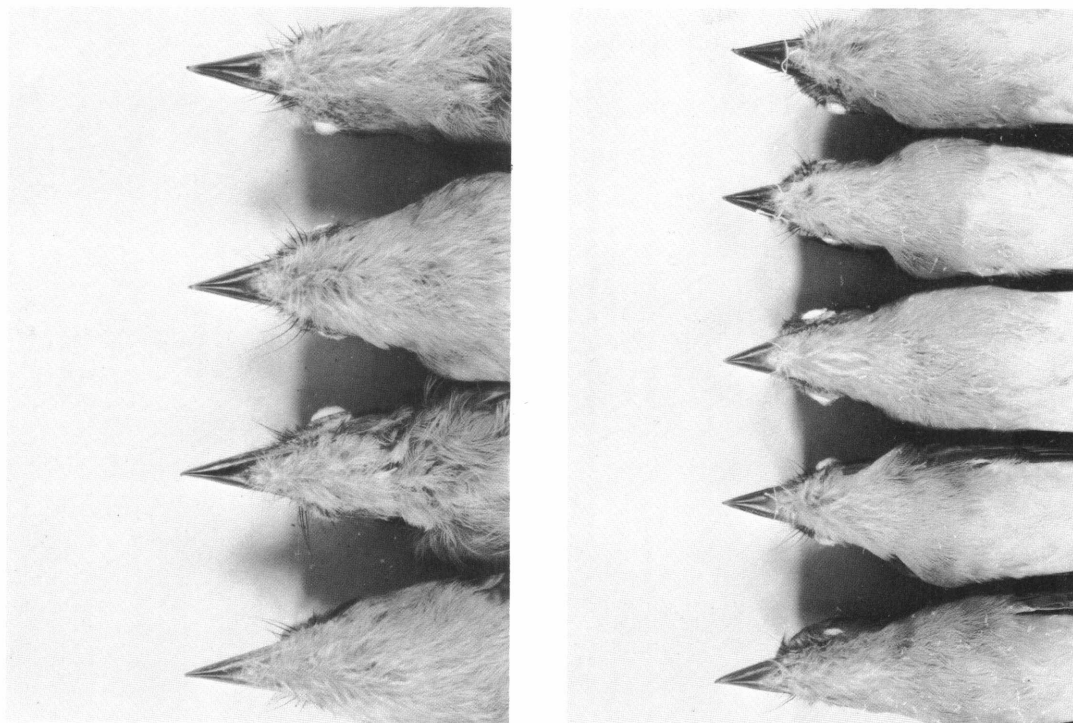


FIG. 21. Mandible becomes paler in color in the older museum specimens of many species of *Myiarchus*, thus rendering this character unreliable except in fresh specimens. Photographs taken in 1973; dates given are years in which specimens were collected. *Left:* (top to bottom) *M. venezuelensis*, AMNH 821999, 1970; AMNH 821987, 1968; PC 59500, 1953; AMNH, 497305, 1901. *Right:* *M. ferox australis*, AMNH 822495, 1970; AMNH 771886, 1958; AMNH 822503, 1962; AMNH 319499, 1930; AMNH 497245, 1900.



FIG. 22. Habitat of *Myiarchus venezuelensis*. *Top*: Deciduous woodland in tropical zone of northeastern Venezuela, near El Callao, Bolívar, May 1970; elevation 150 m. Sympatric with *M. ferox* (intergrades between *ferox* and *brunnescens*) and *M. t. tyrannulus* at this locality. *Bottom*: Hurricane-ravaged woodland along main ridge of island of Tobago, May 1968; elevation 300 m.



FIG. 23. Habitat of *Myiarchus venezuelensis*. *Top*: Deciduous woodland in semi-arid tropical zone of extreme northwestern Venezuela, near Cerro Alto del Cedro, Zulia, May 1970; elevation 200 m. Three other species were recorded and collected only a few kilometers from this locality: *M. p. panamensis*, *M. tuberculifer pallidus*, and *M. t. tyrannulus*. *Bottom*: Deciduous woodland (on the slopes) overlooking a cocoa plantation in the semi-arid tropical zone of coastal Venezuela, near Ocumare de la Costa, May 1968; elevation 100 m. *M. venezuelensis* showed a preference for cocoa plantation, whereas *M. t. tyrannulus* had territories on drier slopes.

gua, Venezuela, five pairs; Bolívar, Venezuela, five pairs; Tobago, West Indies, four pairs.

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 24 and 25.

In response to playback, or when excited by intruding conspecifics, *M. venezuelensis* vocalizes with repeated hiccups, rasps, rasp-whistles, and "wheer-r-r" notes. The hiccups are noisier to the human ear than are those of *M. tuberculifer*, and the traces on the spectrograms (fig. 25) reveal this random noise, with energy distributed over a large range of frequencies. The two syllables normally are displayed as sharp glissandos rather than chevron-like "huit" notes. The rasps are often given in rapid sequence, without the intervention of other calls, or may be followed immediately by whistles, either continuously or discontinuously. The normal and frequent use of rasp-whistles under these circumstances is diagnostic, as is the complete absence of rolls. The "wheer-r-r" note is similar to that of *M. tuberculifer*, the only other species for which I have recorded this distinctive and easily recognizable call.

Foraging birds not excited by playback or

intruding conspecifics will render prolonged, plaintive whistles with little frequency excursion. In my sample they varied in duration from 0.6 to 1.5 seconds. Presumably these calls serve as location notes in the communication between paired birds. Sometimes they were given in response to the removal of the mate by collecting or to the termination of playback of a recording of this species' repertoire. "Huit" notes apparently are absent completely from the repertoire.

DAWN SONG: The dawn song of the male of *M. venezuelensis* (fig. 24) consists exclusively of isolated, plaintive whistles identical with those given by foraging birds during the daylight hours. The only characteristics of the dawn song that set it apart from the daytime rendition of whistles are its repeated delivery from one perch and the total preoccupation of the male with singing as opposed to foraging for food and maintaining visual or auditory contact with his mate. The time interval between whistles is quite variable: in samples recorded from Bolívar, Tobago, and Aragua, the interval averaged 4, 8, and 10 seconds, respectively. I have heard no "huit" notes in the dawn song of this species.

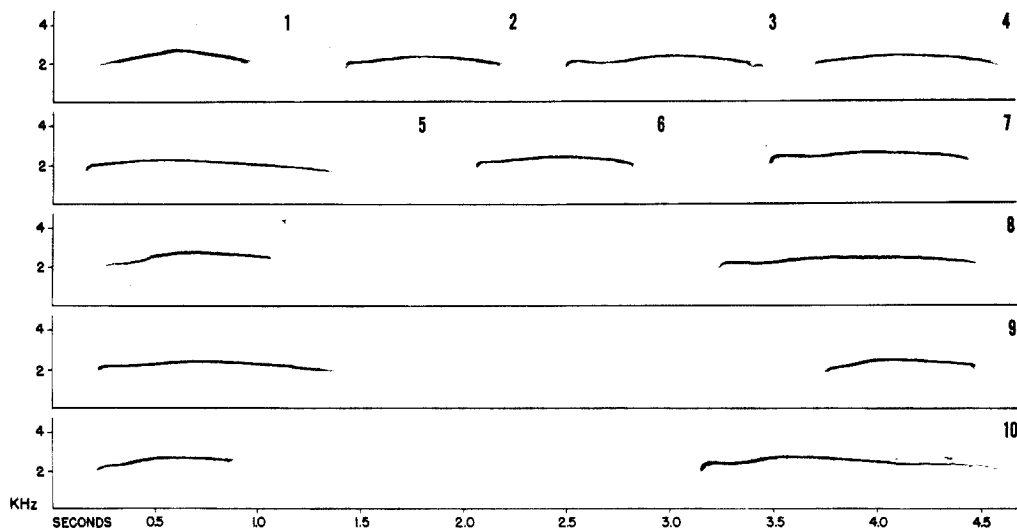


FIG. 24. Variation in vocal characters of *Myiarchus venezuelensis*: whistles (1-7) and dawn song (8-10). Spectrograms were made with 45 Hz. filter and are from recordings made in Venezuela (1, Zulia; 2, 3, Yaracuy; 4, 8, Aragua; 5, 9, Bolívar) and Tobago (6, 7, 10).

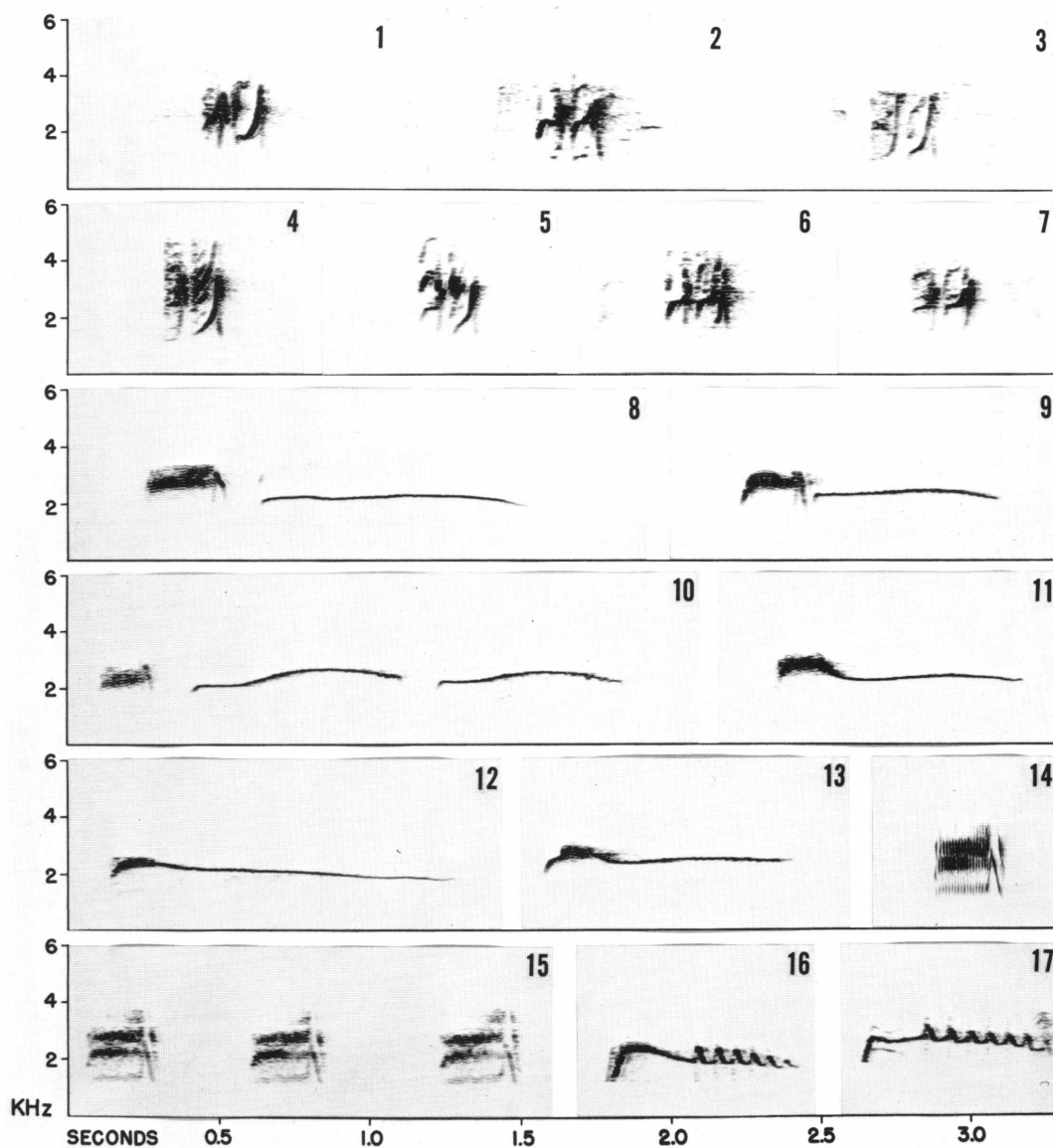


FIG. 25. Variation in vocal characters of *Myiarchus venezuelensis*: hiccups, rasp-whistles, rasps, and "wheer-r-r" notes. Spectrograms are from recordings made in Venezuela (1, 9, 11, Zulia; 2, 3, 14, 15, Yacuy; 4, 10, Aragua; 5, 12, 16, Bolívar) and Tobago (6, 7, 8, 13, 17). The 300 Hz. filter was used for 14 only.

GEOGRAPHICAL VARIATION: There is no evidence in my samples, which include recordings from the isolated population on Tobago, to suggest that there is geographical variation in any of the vocal characters of *M. venezuelensis*.

ITINERARY OF FIELDWORK

1968—April 27 through May 1, near Ocumare de la Costa, Aragua, Venezuela; May 20-22, near Upata, Bolívar, Venezuela; May 24-29, on Tobago, in the West Indies.

1970—April 30 through May 6, near Upata and El Callao, Bolívar, Venezuela; May 14-15, near Cerro Alto del Cedro, Zulia, Venezuela.

1974—May 7, near Nirgua, Yaracuy, Venezuela.

SYSTEMATICS

Myiarchus venezuelensis Lawrence

Myiarchus venezuelensis Lawrence, 1865, p. 38 (type locality, "Venezuela"; holotype in the American Museum of Natural History, examined). French, 1973, p. 321. Morony, Bock and Farrand, 1975, p. 81. Haffer, 1975, p. 140. Meyer de Schauensee and Phelps, 1978, p. 256.

Myiarchus ferox insulicola Hellmayr and Seilern, 1915, p. 202 (type locality, Tobago; holotype in the Munich Museum). Oberholser, 1918, p. 305. Hellmayr, 1927, p. 178 (synonymy). Zimmer, 1938a, p. 12. Junge and Mees, 1958, p. 108. Meyer de Schauensee, 1966, p. 350 (in first addenda).

Myiarchus ferox ferox: Todd, 1922, p. 200 (in part, Tobago).

Myiarchus ferox venezuelensis: Berlepsch, 1907, p. 477 (new combination). Oberholser, 1918, p. 305. Todd, 1922, p. 203 (in part). Hellmayr, 1927, p. 178 (synonymy). Zimmer, 1938a, p. 15. Wetmore, 1953, p. 12. Phelps and Phelps, 1963, p. 189 (designate Lago de Valencia as the type locality). Haffer and Borrero, 1965, p. 43. Meyer de Schauensee, 1966, p. 350.

Myiarchus ferox panamensis: Dugand, 1947, p. 622 (in part, Los Pendales). Meyer de Schauensee, 1950, p. 826 (in part, Los Pendales, Caracolicito).

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 26): Known only from the tropical zone (up to 600 m.) of northeastern Colombia (Atlántico, Bolívar, Magdalena, Guajira), northern Venezuela (Zulia eastward to the Distrito Federal, and from northeastern Bolívar between Upata and El Callao), and the island of Tobago.

The congener that most frequently occurs sympatrically throughout the range of *M. venezuelensis* is *M. tyrannulus*. There is more limited sympatry with *M. tuberculifer* in ecotonal habitats, because the latter species prefers a more mesic environment. There is local sympatry with *M. panamensis* in northeastern Colombia and extreme northwestern Venezuela, and with *M. ferox* in northeastern Bolívar, Venezuela.

Specimens examined, 78; localities, by country, from north to south and west to east (see fig. 26; asterisks denote author's study areas): COLOMBIA, Nazaret, Guajira; Los Pendales, Atlántico (Turbaco, Bolívar); Caracolicito, Magdalena; Cansona, Bolívar (Colosó, Sucre); "Camp Costa Rica," Magdalena; Villa Felisa, Norte de Santander (Cúcuta; Los Patios). VENEZUELA, *Cerro Alto del Cedro, Zulia (La Esperanza); Mirimire, Falcón; Las Trincheras, Carabobo (Lago de Valencia; Urama; San Esteban; Puerto de la Cruz, Distrito Federal); *Ocumare de la Costa, Aragua (Turiamo; Cata); *Nirgua, Yaracuy (El Hacha, Lara); Santa Lucía, Miranda; Pie de Cuesta, Lara; *Upata, Bolívar (El Callao; El Palmar; El Manteco). *TOBAGO.

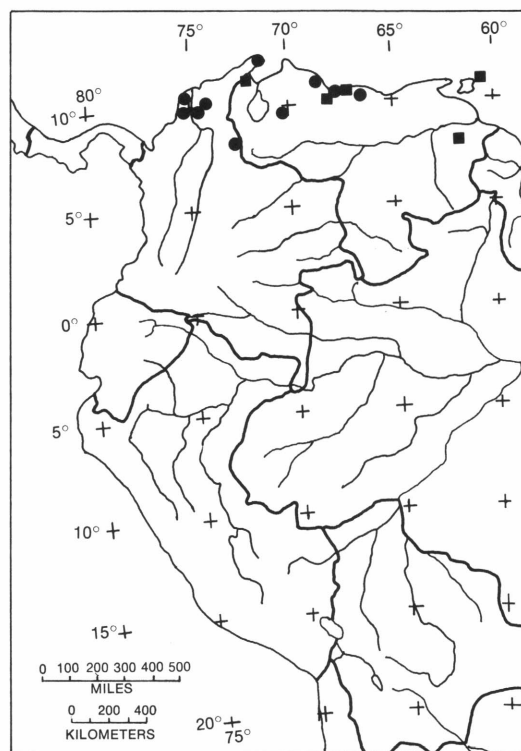


FIG. 26. Distribution of *Myiarchus venezuelensis* as indicated by localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). See page 494 for a list of these localities and page 493 for an itinerary of author's field work with this taxon.

RELATIONSHIP OF

venezuelensis WITH *Myiarchus ferox*

Lawrence (1865) originally described *venezuelensis* as a full species, largely because of the extent of the "rufous margins" of the rectrices. Oberholser (1918), in his revision of the subspecies of *M. ferox*, regarded *venezuelensis* as "without a doubt a subspecies of *Myiarchus ferox*, and its representative in western Venezuela and eastern Colombia." Todd (1922) followed Oberholser, and attributed the rufous margins of the rectrices to immaturity, thereby misinterpreting one of the diagnostic characteristics of this species. Hellmayr (1927), though aware of Todd's error, agreed that it should be treated as a representative form of *M. ferox*, thus extending the range of that species northward to the coast of Venezuela. Hellmayr correctly pointed out that *venezuelensis* is morphologically nearest to that population of *M. ferox* occupying the Orinoco basin. All recent workers, including Zimmer (MS) and Phelps and Phelps (1950, 1963), have followed Hellmayr.

The Tobago population, "*insulicola*" (Hellmayr and Seilern, 1915), is not separable, morphologically or vocally, from *venezuelensis*. Of this form Hellmayr (1927) wrote: "... perhaps not properly separable from *M. f. venezuelensis*, though it should be recalled that no representative of this group of Flycatchers [*M. ferox*] has been found either in Trinidad or on the opposite Venezuelan coast of Bermudez. The Tobago form has, however, nothing to do with typical *M. f. ferox* which lacks the pale brown outer web and the rufous edges to the rectrices, besides several other distinctions. *M. f. venezuelensis* and *M. f. insulicola*, by retaining the rufous markings on wings and tail in adult plumage, stand apart from the other races." Zimmer (MS) had no opportunity to examine specimens from Tobago, and followed Hellmayr.

The true relationship of *venezuelensis* and the species *ferox* was obscured for years by the scarcity of specimens of *venezuelensis* and the lack of distributional information, and by the difficulty in making a morphological distinction between *venezuelensis* and the Orinocan *ferox* alluded to above (see p. 575 for more detail).

Furthermore, *venezuelensis* appeared to provide a natural link to *panamensis* in Colombia, also considered a representative of the species *ferox*; thus the argument to treat *venezuelensis* as a subspecies of *M. ferox* seemed eminently sound on a zoogeographical basis.

I relate here in some detail the sequence of events that led to my discovery that *venezuelensis* is, in fact, specifically distinct from *M. ferox*, for it provides what I regard a notable example of the importance of vocal characters as an early warning system for the detection of cryptic species and as additional clues in determining specific limits within a group in which morphological characters may be misleading or equivocal.

At the time of my first trip to Venezuela in 1968, I had no previous field experience with any population of *M. ferox*, so that species was vocally unknown to me. I chose to work first with *venezuelensis* because Paul Schwartz, the leading field ornithologist in Venezuela, had alerted me to a readily accessible population in Aragua. In view of the scarcity of *venezuelensis* in collections, I was surprised at the numbers that I found near Ocumare de la Costa; I was able to get sound recordings and a good series of specimens of known voice. At that time, the only other locality at which Schwartz had had field experience with *Myiarchus* having the same voice as that of the Aragua birds was near Upata, in northeastern Bolívar. Since specimens from that region had been assigned to nominate *ferox* (Phelps and Phelps, 1963; Zimmer, MS) and since he had no reason to suspect otherwise, Schwartz assumed that his specimens from Upata were *ferox*. I visited the same locality, also in 1968, and obtained a small series of birds of known voice, using a playback tape that I had prepared from the recordings of *venezuelensis* in Aragua. The Upata birds that I collected were vocally identical with those in Aragua and, without making a critical morphological analysis at the time, I, too, assumed that these must be nominate *ferox*, based on the ranges given in the literature.

During my second trip to Venezuela in 1969, I became familiar with *M. ferox brunescens* in the llanos, and established that it

was very different vocally from *venezuelensis* and clearly not conspecific. Subsequent examination of specimens throughout the middle and lower Orinoco basin revealed that *M. ferox* of eastern Venezuela can best be described as intermediate between *brunnescens* (of the llanos) and nominate *ferox* (of the Amazon basin); there is a detailed discussion of this intergradation on page 575. All but one of the specimens in the Phelps Collection taken in the Upata region of Bolívar were examples of this intermediate population. The exception (PC 17863) is a specimen of *venezuelensis* taken at El Palmar, but incorrectly identified as *ferox*. I then reexamined the Upata specimens Schwartz and I had collected, and they also proved to be *venezuelensis*. Not only was there now evidence, morphological and vocal, for removing *venezuelensis* from *M. ferox*, there was also a strong implication that *venezuelensis* and *M. ferox* might actually be sympatric in north-eastern Bolívar.

To confirm this presumed sympatry I revisited the Upata region in 1970. At localities where I had been able to attract and collect only *venezuelensis* in 1968, since my only available reconnaissance tape then was one made from *venezuelensis* in Aragua, I succeeded in calling in, recording, and collecting a series of *M. ferox*, using a reconnaissance tape prepared from recordings made of *M. f. brunnescens* the previous year. Sympatry was established at several localities along the highway between Upata and Tumeremo, near El Palmar, and between 50 and 70 km. S of Upata on the highway to El Manteco. Because of this sympatry and the morphological and vocal differences, *venezuelensis* should be considered specifically distinct from the species *ferox*.

RELATIONSHIP OF *venezuelensis* WITH *panamensis*

Until the release of information (Morony, Bock and Farrand, 1975; Ridgely, 1976; Meyer de Schauensee and Phelps, 1978) obtained in my study, the relationship between *venezuelensis* and *panamensis* had been interpreted by all recent authors to be that between conspecific and contiguous representative forms of a single species, *M. ferox*. Both forms, superficially at

least, complete a morphological gradient from dark nominate *ferox* to pale *panamensis*, and treating them in this manner would extend the range of *M. ferox* through Venezuela and Colombia, and northward into Costa Rica. Oberholser (1918), in his review of the subspecies of *M. ferox*, wrote of *panamensis*: "... clearly but a subspecies of *Myiarchus ferox ferox*, being connected with that form through *Myiarchus ferox venezuelensis*." There has been some confusion, however, in assigning certain specimens taken in northwestern Venezuela and in northern Colombia, and these difficulties, coupled with the scarcity of specimens of either form in this critical zone of potential contact, led to incompatible statements of the ranges of the two forms. Phelps and Phelps (1963), for example, had *panamensis* extending eastward in Venezuela as far as eastern Zulia and western Merida, whereas Meyer de Schauensee (1964) had *venezuelensis* extending westward into Guajira, Colombia, an apparent overlap of these "races" of some 250 km.

It was Paul Schwartz who first caused me to doubt seriously that *venezuelensis* and *panamensis* were conspecific. As mentioned above, Schwartz' only field experience with "*ferox*" was with *venezuelensis* in Bolívar. During my first visit to Venezuela in 1968 Schwartz and I were comparing recordings that we had made of this form, and he pointed out that the vocal repertoire of *venezuelensis* was quite different from that of *panamensis* as represented in some recordings made by L. Irby Davis in Panama. I was able to confirm this difference, to reinforce it with morphological differences, and eventually to establish sympatry between *M. venezuelensis* and *M. panamensis* by collecting both forms at a single locality (near Cerro Alto del Cedro along the Colombian border of Venezuela).

I re-examined specimens in the Phelps Collection and discovered that PC 59500, also from near Cerro Alto del Cedro and tentatively identified as "*panamensis* (?)," is actually *M. venezuelensis*. Three other specimens (PC 63292-63294) taken in the same general area are also *M. panamensis*, thus providing additional evidence of sympatry of *M. venezuelensis* and *M. panamensis*.

Specimens that have come to my attention subsequent to my fieldwork in Venezuela and Colombia indicate that sympatry between *M. venezuelensis* and *M. panamensis* is by no means restricted to northwestern Venezuela. Wetmore (1953) was the first to record *venezuelensis* in Colombia, on the basis of one specimen taken in 1941 on the Guajira peninsula, though he did not appreciate its specific status at the time. Dugand (1947) discussed four specimens from northern Colombia (Caracalico, in Magdalena, and Los Pendales, in Atlántico) that he had assigned, with difficulty, to *panamensis*, and quoted correspondence from William H. Phelps, Sr., of Caracas, who concurred with this determination somewhat reluctantly, "... because of geography. They are within the range of *panamensis* as given by several authors." Meyer de Schauensee (1950) also agreed. When Haffer (Haffer and Borrero, 1965) collected *venezuelensis* at Cansoma, Bolívar, Colombia in 1960, he was prompted to reexamine the four specimens that Dugand had discussed and he identified all four as *venezuelensis*. That he had obtained this "race" of "*M. ferox*" at almost the same locality as a specimen of *panamensis*, another "race" of "*M. ferox*," he thought might be explained by an autumn movement of *venezuelensis* southward from its main range. But when Haffer learned of my conclusion that *venezuelensis* was specifically distinct from *M. ferox* (in Morony, Bock and Farrand, 1975), he acknowledged the possibility that *M. venezuelensis* and *M. panamensis* might in fact be sympatric in the area where he had worked (Haffer, 1975). I have subsequently examined all six of these specimens from Colombia and have confirmed their identity as *M. venezuelensis*.

Because of this sympatry and the morphological and vocal differences, *venezuelensis* should be considered specifically distinct from *panamensis*.

REMARKS: Four of the six Colombian specimens are in reasonably fresh plumage (September and January) and appear to be paler above than three comparably plumaged specimens from Venezuela. I would prefer to see a better series of fresh-plumaged material from throughout the range, however, before commenting further on geographical variation.

The apparently disjunct pattern of the present range of *M. venezuelensis* (fig. 26) deserves more comment. It is probable that some of the apparent interruptions in the range of this species along the northern tier of Venezuelan states are artifacts and that more extensive work may establish new localities, particularly in northern Zulia and western Falcón. On the other hand, the avifauna of Trinidad is well known and it is inconceivable to me that a population of *M. venezuelensis* could exist there at the present time and not have shown up in the many collections made on the island. In 1970 I made a transect from northeastern Bolívar, where the species is well established, through the states of Monagas, Sucre, and Anzoátegui, and failed to attract *venezuelensis* with my reconnaissance tape. Furthermore, the Phelps have made extensive collections in northeastern Venezuela, particularly in Sucre, without taking this species.

The presence of a well-established population of *M. venezuelensis* on Tobago, together with its absence from Trinidad and the adjacent coast of Venezuela, suggests that the species may once have occupied a more extensive portion of the northern cordillera, including what are now the islands of Trinidad and Tobago, and that subsequent extinctions due to changes in climate, habitat, and land-use have resulted in the disjunctions in distribution evident today. The present restriction in range may be due in part to a rather narrow habitat tolerance. The population in northeastern Bolívar, for example, is associated with the relatively narrow zone of deciduous woodland separating the more xeric savannas (llanos) to the west and the more mesic evergreen forest to the east and south.

Since I was able to establish that *M. venezuelensis* does occur sympatrically with both *M. panamensis* and *M. ferox*, there was no need to rely on simulating sympatry through the use of playback experiments, as was done with the *M. tuberculifer* complex and other groups. Moreover, *M. venezuelensis* differs greatly from both *M. panamensis* and *M. ferox* with respect to vocal characters, and it was not surprising to find that *venezuelensis* can discriminate between its own repertoire and those of the other two. The reciprocal ability, i.e.,

that of *M. panamensis* to discriminate between its own voice and that of *M. venezuelensis*, is illustrated by a series of playback experiments with a territorial pair of *M. panamensis* in Colombia, which I have described on p. 562. Likewise, the playback experiments described on p. 578 illustrate the failure of a territorial pair of *M. ferox* to respond to playback of a tape of the vocal repertoire of *M. venezuelensis*.

Playback experiments conducted in Aragua, Venezuela, and on Tobago revealed that *M. venezuelensis* would not respond to playback of the repertoires of five congeners, including the two species (*M. tuberculifer* and *M. swainsoni*) that show the closest similarity in vocal characters. The following field notes, made on April 30, 1968, illustrate this discriminatory ability in a pair of breeding *M. venezuelensis*:

Experiment 24—cocoa plantation, near Ocumare de la Costa, Aragua. Tapes used, *venezuelensis* vs. *swainsoni* (Brazil). Pair silent, location unknown at start. Start at 9:10 A.M. Within one minute, one bird showed 50 ft. from *venezuelensis* model. Down to 10 feet at 9:13, calling well. Out to 15 ft., giving rasping notes. Crisscross at 9:14. Another crisscross. Both birds now within 20 ft. of *venezuelensis* model. "Study" at 6 ft., both calling well. One still in 6 ft. "study" at 9:15; at 6 ft. and 8 ft. "studies" at 9:16. Both still there at cable switch. To midpoint in 30 seconds, then both to 30 ft. of new *venezuelensis* model by 9:18. Crisscross at 9:20. Crisscross, and to 15 ft. of *venezuelensis* model. Another crisscross. Another crisscross at 9:23. To midpoint at 9:24, and end of experiment.

Experiment 25—same locality, pair, and date as above. Tapes used, *M. tyrannulus* (Curaçao) vs. *atriceps* (Argentina). Pair out of experimental area at start at 9:25 A.M. One showed at 30 ft. of *tyrannulus* model, momentarily, then left experimental area. Occasional calling outside experimental area. At 9:29, one perched 30 ft. from *atriceps* model, then flew out of area. No response; discontinued experiment after seven minutes.

Experiment 26—same locality, pair, and date as above. Tapes used, *venezuelensis* vs. Middle American *tuberculifer*. Start at 9:36 A.M. Both appeared from out of experimental area, to midpoint at 9:39. Down to 40 ft. of *venezuelensis* model at 9:43. Remained there at cable switch. To 6 ft. of new *tuberculifer* in 20 seconds. Over to 30 ft. from new *venezuelensis* model at 9:44. Crisscross at 9:45. Perched 30 ft. over *venezuelensis* model. One at 30 ft., other at 50 ft. from *venezuelensis* model at 9:47. In to 6 ft. at 9:49, calling well. Out to midpoint at 9:50, then back to 30 ft. of *venezuelensis* model. Then in to 8 ft. of model, calling well, at end of experiment.

Experiment 27—same locality, pair, and date as above. Tapes used, *venezuelensis* vs. *swainsoni* (Brazil). Given 15 minute rest after last experiment. Pair silent, location unknown at start at 10:04 A.M. One bird showed at 30 ft. from *venezuelensis* model within 30 seconds, calling well. Crisscross at 10:07. Both birds within 40 ft. of *venezuelensis* model at cable switch. One to midpoint in 30 seconds. Flew across new *venezuelensis* area. Back over to 30 ft. of new *swainsoni* model at 10:14. Crisscross over *venezuelensis* model at 10:16. Response has waned somewhat since experiment 24. Fair response to *venezuelensis*, no response to *swainsoni*.

MYIARCHUS SWAINSONI CABANIS AND HEINE

This endemic but widespread South American species is found in much of the tropical zone of South America east of the Andes and south into the subtropical zone of Uruguay and central Argentina.

The species is polytypic and four subspecies are admitted here: *swainsoni*, *pelzelni*, *ferocior*, and *phaeonotus*. It is unique among its South American congeners in that certain populations are migratory.

Myiarchus swainsoni is noteworthy in that its subspecies have diverged from each other morphologically and vocally to a greater extent than in any other South American *Myiarchus*

except *M. tuberculifer*. It is easier, for example, to distinguish between specimens of *M. s. pelzelni* and *M. s. phaeonotus* than to assign many specimens to either *M. swainsoni* or *M. ferox*. It is understandable, then, that this unusual geographical variation led to considerable confusion and controversy over the specific limits of *M. swainsoni*, and particularly as to whether *pelzelni* and *phaeonotus*, the morphological extremes, should be included. These points are discussed in greater detail in separate sections.

DIAGNOSIS: One of the larger (see measurements in tables 22 and 23) "dark-tailed" spe-

cies, i.e., having rectrices of adults not conspicuously marked with Antique Brown (other than fringing in fresh plumage in some populations) and without conspicuous whitish tips. Coloration of crown uniform throughout and not noticeably contrasting with that of the back. Tail relatively short, compared to length of wing: ratio of tail length to wing length usually 92 percent or less (down to 81%) and

rarely more than 93 percent. Wing pointed: ninth primary usually at least 1 mm. longer than fifth (up to 8 mm. longer), and rarely shorter than fifth; fourth primary usually no more than 5 mm. longer than tenth (may be as much as 4 mm. shorter), and rarely more than 6 mm. longer than tenth. In fresh specimens, color of mandible variable geographically (a subspecific character) from black to brown, and

TABLE 21
Measurements (in Millimeters and Grams) in Samples of *Myiarchus venezuelensis*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	29	87 - 97	93.3 ± 0.40	2.14	2.29
Females	37	85 - 93	88.2 ± 0.31	1.90	2.16
Tail Length					
Males	29	82 - 94	89.5 ± 0.45	2.40	2.68
Females	37	80 - 89	84.2 ± 0.38	2.31	2.74
Body Weight					
Males	4	27.0 - 32.0	29.3 ± 1.03	2.06	7.04
Females	6	27.0 - 33.0	30.2 ± 0.92	2.25	7.46

TABLE 22
Wing Length (in Millimeters) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. s. swainsoni</i>					
Males	230	88 - 99	94.0 ± 0.15	2.27	2.41
Females	188	83 - 95	88.9 ± 0.17	2.34	2.63
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	45	90 - 102	96.8 ± 0.40	2.65	2.74
Females	23	87 - 99	91.8 ± 0.62	2.97	3.23
<i>M. s. ferocior</i>					
Males	101	91 - 104	98.7 ± 0.28	2.81	2.84
Females	39	89 - 101	93.8 ± 0.52	3.24	3.45
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	8	93 - 101	96.5 ± 0.96	2.73	2.82
Females	7	88 - 92	89.4 ± 0.53	1.40	1.56
<i>M. s. pelzelni</i>					
Males	32	87 - 97	91.6 ± 0.49	2.76	3.01
Females	28	81 - 95	87.1 ± 0.56	2.97	3.41
Intergrades between <i>pelzelni</i> and <i>phaeonotus</i>					
Males	27	84 - 93	89.0 ± 0.38	1.95	2.19
Females	15	82 - 89	85.3 ± 0.64	2.50	2.93
<i>M. s. phaeonotus</i>					
Males	34	84 - 94	90.0 ± 0.37	2.17	2.41
Females	33	80 - 90	85.4 ± 0.42	2.41	2.82

TABLE 23
Tail Length (in Millimeters) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. s. swainsoni</i>					
Males	231	76 - 91	83.8 ± 0.18	2.70	3.22
Females	188	71 - 87	79.7 ± 0.20	2.74	3.43
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	45	81 - 92	86.3 ± 0.36	2.42	2.80
Females	22	76 - 87	82.8 ± 0.63	2.96	3.57
<i>M. s. ferocior</i>					
Males	100	80 - 94	87.9 ± 0.26	2.63	2.99
Females	38	77 - 91	83.6 ± 0.56	3.45	4.13
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	8	79 - 92	85.4 ± 1.46	4.14	4.85
Females	7	80 - 82	80.9 ± 0.34	0.90	1.11
<i>M. s. pelzelni</i>					
Males	34	77 - 88	82.1 ± 0.46	2.70	3.29
Females	28	73 - 85	77.8 ± 0.46	2.42	3.12
Intergrades between <i>pelzelni</i> and <i>phaeonorotus</i>					
Males	27	77 - 84	80.3 ± 0.36	1.86	2.32
Females	15	72 - 82	76.1 ± 0.81	3.15	4.14
<i>M. s. phaeonorotus</i>					
Males	34	76 - 86	80.6 ± 0.47	2.75	3.42
Females	33	71 - 82	76.3 ± 0.48	2.73	3.58

color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics includes repeated rolls that are closely associated with rasps, but there are no "wheel-r-r" notes. Dawn song consists of alternated renditions of plaintive whistles, "huit" notes, and more complex phrases.

HABITAT (FIGS. 27-29, 64, 78): As a species, *M. swainsoni* is found in a greater range of xeric to mesic habitats than any other South American *Myiarchus* except *M. tuberculifer*. Most populations are to be looked for in clearings in wooded areas, borders of woodlands, wooded areas along rivers and streams, disturbed agricultural areas, and wooded savannas. The most mesic habitats are occupied by *phaeonorotus* in Venezuela, where the wooded slopes of the tepuis, and clearings in rather moist tropical forest, are favored sites. At the other extreme is *ferocior*, a bird of the dry chaco woodlands of Bolivia and Argentina.

Myiarchus swainsoni is typically a species of low, tropical elevations throughout the Amazon basin. Along the eastern edge of the Andes, however, I found *pelzelni* as high as 1200 m. in the Urubamba valley of Peru and *ferocior* as high as 800 m. in the lower subtropical woodlands of Tucumán, Argentina. Crossin took breeding *ferocior* (FMNH 294124 and 294125) at the edge of the Bolivian chaco as high as 1200 m. A Carriker specimen of *ferocior* (ANSP 135715, misidentified as "*cephalotes*") was taken as a breeding bird at Tomina, Bolivia, according to the label. The habitat at this locality, "thorny trees, bushes and cacti" (Bond and Meyer de Schauensee, 1942), is suitable but the elevation of 2000 m. given on the label seems too high for breeding *ferocior*; the specimen may actually have been collected some distance nearer the Río Grande, which flows into the Bolivian chaco. That migrants may reach higher elevations is suggested



FIG. 27. *Top*: Habitat of *Myiarchus swainsoni swainsoni* in deciduous woodlands in the Sierra de Animas, Maldonado, Uruguay, December 1967; elevation 200 m. *Bottom*: Habitat of *M. swainsoni pelzelni* in deciduous woodlands and coffee plantations in the semi-arid subtropical zone along the Río Urubamba, Cuzco, Peru, November 1972; elevation 1100 m. Sympatric with *M. f. ferox* and *M. t. tyrannulus* at this locality.

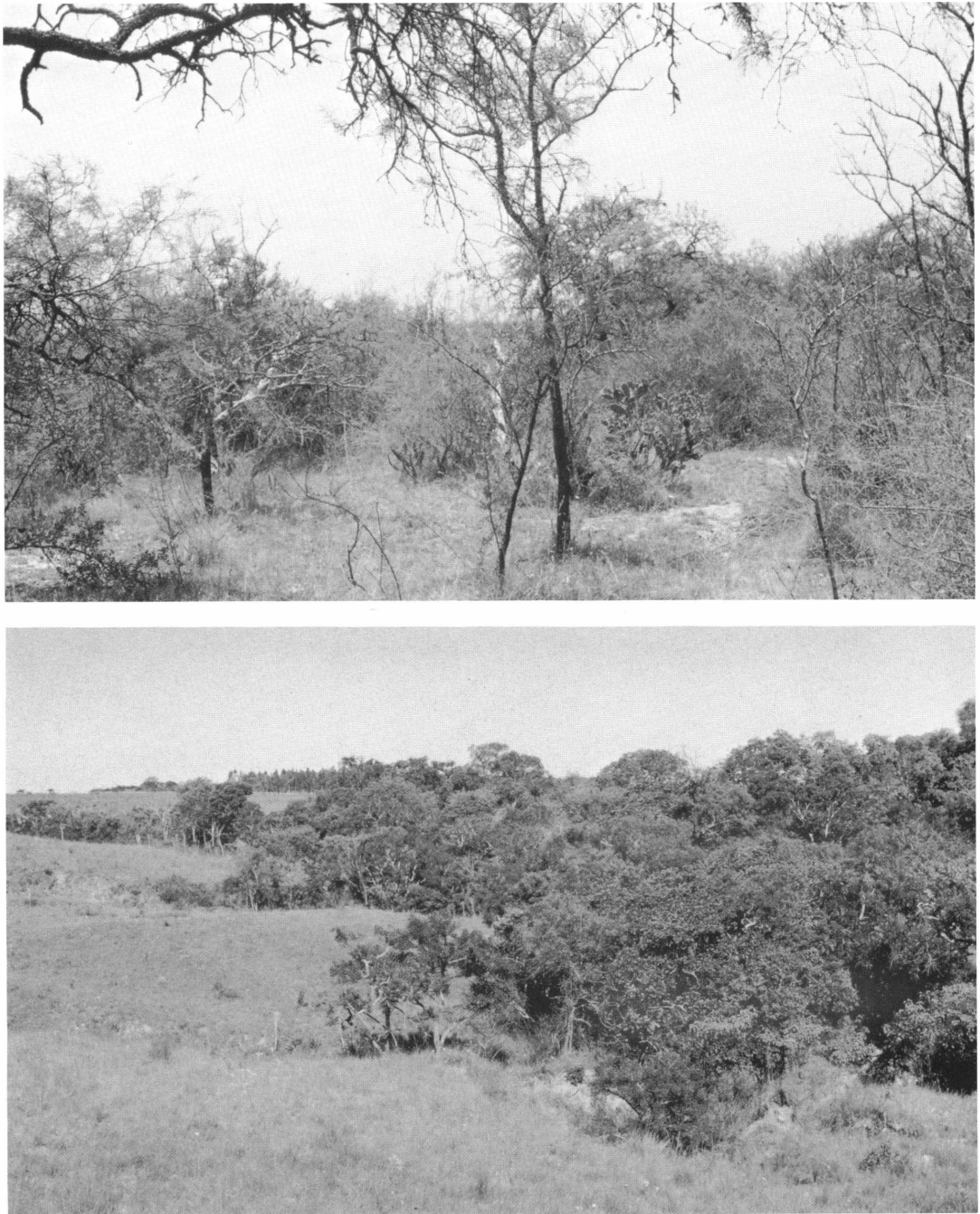


FIG. 28. *Top*: Habitat of *Myiarchus swainsoni ferocior* in deciduous woodland of the chaco of Argentina, along the Río Salado, in Santa Fé, December 1970; elevation 50 m. Sympatric with *M. t. tyrannulus* at this locality. *Bottom*: Habitat of *Myiarchus swainsoni* (intergrades between *swainsoni* and *ferocior*) in deciduous woodlands along a creek at Las Tres Marías, Corrientes, Argentina, November 1970; elevation 75 m. Sympatric with *M. ferox australis* and *M. t. tyrannulus* at this locality near the Río Paraná.

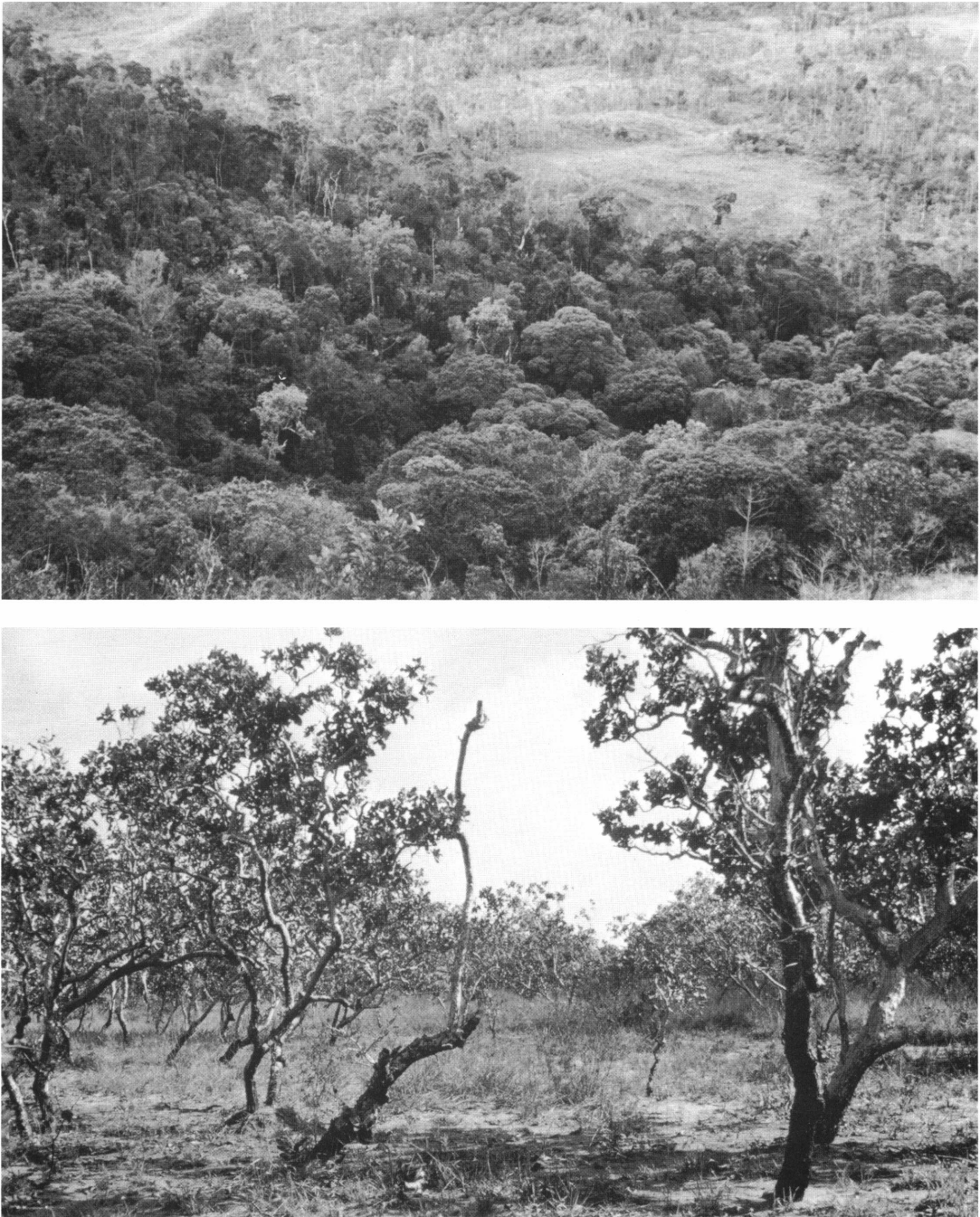


FIG. 29. *Top*: Habitat of *Myiarchus swainsoni phaeonotus* at edge of humid, tropical forest at Kavanayén, Bolívar, Venezuela, May 1969; elevation 1200 m. Sympatric with *M. t. tuberculifer* at this locality. *Bottom*: Habitat of *Myiarchus swainsoni* (intergrades between *phaeonotus* and *pelzelni*) in an open woodland of *Curatella americana* on the Hannover savanna hear Zanderij, Surinam, December 1970; elevation 50 m. Sympatric with *M. f. ferox* at this locality.

TABLE 24
Ratio of Tail Length to Wing Length (in Percentage) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. s. swainsoni</i>					
Males	230	85 - 95	89.2 ± 0.13	1.97	2.21
Females	187	83 - 95	89.7 ± 0.15	2.07	2.31
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	45	86 - 93	89.2 ± 0.24	1.62	1.82
Females	22	85 - 92	90.1 ± 0.34	1.61	1.79
<i>M. s. ferocior</i>					
Males	100	85 - 94	89.1 ± 0.20	2.01	2.25
Females	37	85 - 94	89.1 ± 0.38	2.29	2.57
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	8	85 - 93	88.3 ± 0.84	2.38	2.69
Females	7	89 - 92	90.4 ± 0.37	0.98	1.08
<i>M. s. pelzelni</i>					
Males	32	85 - 93	89.7 ± 0.42	2.39	2.66
Females	28	81 - 93	89.1 ± 0.43	2.28	2.56
Intergrades between <i>pelzelni</i> and <i>phaeonotus</i>					
Males	26	87 - 92	90.3 ± 0.28	1.43	1.58
Females	15	87 - 92	89.1 ± 0.43	1.67	1.87
<i>M. s. phaeonotus</i>					
Males	34	86 - 93	89.6 ± 0.26	1.52	1.70
Females	32	85 - 93	89.3 ± 0.32	1.82	2.04
All Subspecies of <i>M. swainsoni</i>					
Males	475	85 - 95	89.3 ± 0.09	1.95	2.18
Females	328	81 - 95	89.6 ± 0.11	2.04	2.28
Both Sexes	803	81 - 95	89.4 ± 0.07	1.99	2.23

by a Steinbach specimen of *swainsoni* (FMNH 181198) taken at Tiraque, Bolivia, on March 13. The Steinbach specimens from this locality bear elevations above 3000 m. There are specimens of *phaeonotus* in the Phelps Collection taken up to 1800 m. on the tepuis of Venezuela.

BREEDING AND ANNUAL CYCLE: The species nests in cavities and uses nesting materials similar to those of other members of the genus. The only nest found by me was in a knothole in a living tree at the edge of a stream (*ferocior*, near Tucumán, Argentina; fig. 30). The hole was approximately 9 m. aboveground; the contents were not determined. Barrows (1883) found a nest near Concepción, Argentina (*swainsoni* × *ferocior*) on December 28: . . . "loose nest of hair, feathers, etc., in a hollow stub five feet from the ground. It contained

three eggs which in color and markings were precisely like those of *M. crinitus*, but a little smaller." Hartert and Venturi (1909) found *ferocior* nesting under the roofs of houses (presumably in crevices) as well as in holes in tree trunks.

The three southern subspecies breed from September into early January (*swainsoni* and *ferocior* principally from November into early January, and *pelzelni* from September through December). Thirty-one males taken in November and December had testes that varied in size from 9 to 14 mm. by 3 to 7 mm. Seven males collected from late February to early April had testes that varied in size from 1 to 3 mm. by 1 to 2 mm. Females taken in November and December had enlarged ova, well-developed oviducts, and active brood patches. I observed

a female carrying nesting material near Tucumán, Argentina, on November 16; she was collected subsequently, and had ova up to 2 mm. in size and an abdomen that was becoming edematous. A very recent fledgling was collected in Rio Grande do Sul, Brazil, on December 28.

Correspondingly, on the other side of the equator, in Venezuela the northern subspecies (*phaeonotus*) breeds from February to May. The testes of two males taken in early May varied in size from 9 to 10 mm. by 5 mm. Two females taken at the same time had slightly enlarged ovaries and oviducts.

Myiarchus swainsoni is the only South American species in the genus in which migratory behavior is definitely known to have evolved. Zimmer (1938a, 1938b) was the first to demonstrate this, though Barrows (1883) suspected a migratory tendency in northeastern Argentina. Junge and Mees (1958) correctly interpreted specimens from the island of Trinidad as being wintering individuals of nominate *swainsoni*. The southernmost populations of *swainsoni* and *ferocior* are absent from their breeding grounds during the austral winter, whereas the remaining tropical subspecies, *pelzelni* and *phaeonotus*, and possibly the northernmost populations of *swainsoni* and *ferocior*, are resident throughout the year.

I have seen no specimens of *swainsoni* or *ferocior* collected during the months of May through August south of latitude 25° S. Most significant is the absence of this species in the collections made by William H. Partridge in Misiones, Argentina, during the southern winter. At localities where he took large series of *swainsoni* in the other months of the year, Partridge took only *M. ferox* from May through August.

Myiarchus swainsoni apparently leaves Uruguay by the end of March (MNHM 598 and 599) and Rio Grande do Sul, Brazil, and northern Argentina by late April (MZSP 8858 through 8860; AMNH 771887, 315438; MACN 9184; IML 10111). A migrant collected in eastern Bolivia on March 13 (FMNH 181198) further suggests a northward movement in March. The species first appears on the breeding grounds in northeastern Argentina in early September (MACN 19817, 3677; AMNH 822071)

and in Uruguay in October (MNHN 2086 through 2088). A migrant of nominate *swainsoni* (FMNH 152576) was taken in central Paraguay as late as October 24. Gyldenstolpe (1945a) referred to a specimen taken in mid-October in northern Bolivia, assigning it to nominate *swainsoni*; if correctly identified, this represents yet another late migrant.

The extent to which the northernmost populations of *swainsoni* and *ferocior* are resident is not clear. Certainly, these populations begin their body molt and undergo replacement of remiges earlier (December and January) than do migrants from farther south (February and

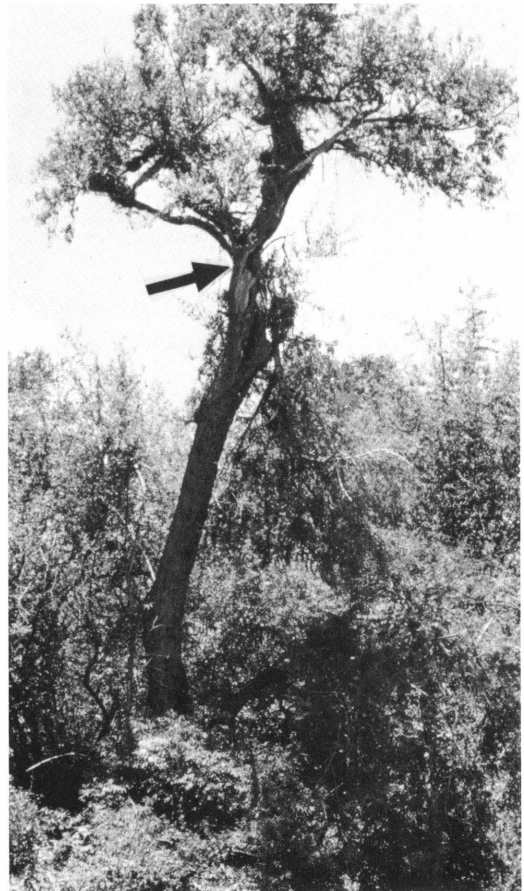


FIG. 30. Tree used as a nest site by *Myiarchus swainsoni ferocior* near Tucumán, Argentina; elevation 500 m. Female (AMNH 822051) was collected on November 16, 1967, as she was carrying nesting material into natural cavity indicated by arrow.

March). A specimen (MZSP 34408) of *swainsoni* taken on May 10 in Rio de Janeiro suggests that at least some individuals in the northern portion of the range of the nominate subspecies are resident birds.

The localities at which wintering or migrant specimens of nominate *swainsoni* have been collected are shown in figure 36. The extreme dates for specimens taken north of the equator are:

Arrival

March 25, Amazonas, Venezuela (PC 38641)

March 27, Rio Branco, Brazil (MZSP 56105)

April 5, Amazonas, Venezuela (AMNH 433238)

Departures

September 4, Bolívar, Venezuela (PC 46409)

September 8, Portuguesa, Venezuela (PC 45586)

September 25, Amazonas, Venezuela (AMNH 497299)

Analysis of the wing lengths of specimens of *swainsoni* taken on the northern wintering grounds indicates that these individuals have the longest wings within the nominate race, and are thus probably representative of the southernmost breeding populations.

I have seen no specimens of *ferocior* taken in Argentina during the months of May through September, and I conclude that most if not all of the southernmost populations of this race migrate. The latest date for Argentina is April 20 (IML 10111). The localities at which wintering or migrant specimens of *ferocior* have been collected are shown in figure 38. There are two additional specimens, not plotted on the map: (1) a specimen (USNM 85100) without date or exact locality, from "E. Peru," and (2) one taken at João Pessoa, in western Amazonas, Brazil, not seen by me but assigned to *ferocior* by Gyldenstolpe (1945b). Unlike wintering nominate *swainsoni*, which seems to spread out over equatorial South America, wintering *ferocior* has been taken only along the western perimeter of the Amazon basin, from central Bolivia to southern Colombia.

Apparently migrant *ferocior* winters farther south than does nominate *swainsoni*. The northernmost specimens of this race have been taken in southern Colombia (AMNH 116690) and eastern Ecuador (uncatalogued specimen, MVZ). Two specimens (ANSP 135710, 135712) taken in Cochabamba, Bolivia, in late July and early August are completing their remige molt, suggesting that they were taken as wintering birds rather than migrants. Migrant *ferocior* may return to the breeding grounds somewhat later than *swainsoni*. Specimens (FMNH 252095, 252098) taken in southeastern Peru in early October have not yet completed their wing molt, and the earliest Argentine specimen (IML 1434) was collected on October 22. A migrant (ANSP 116923) taken in northern Peru on November 18 shows evidence of prealternate molt, and hence was probably several weeks away from the time that it would have been breeding in Argentina.

Juvenals migrate on a schedule approximating that of adults. I have seen eight specimens recognizable as juvenals of nominate *swainsoni* that were taken on the northern wintering grounds. The earliest date in this series is April 5 (AMNH 433238) and the latest date is August 14 (PC 31683). Later dates would be unobtainable, however, because of the impossibility of recognizing a young bird after completion of the postjuvinal molt. Juvenals of *swainsoni* have been taken on the breeding grounds from December 28 (recent fledgling) until April 1. Two migrant *swainsoni* juvenals (FMNH 296254, 296255) taken in southeastern Bolivia on April 4 and 13 further suggest a northward movement in April.

The two migratory subspecies (*swainsoni* and *ferocior*) typically begin their body molt in February or early March, but complete the molt on the wintering ground. It is probable that most of the migrants reach the wintering grounds before they commence replacement of the remiges, for of the 19 specimens taken from March through May, only six had begun to molt remiges and these were all taken in May. All specimens taken on the northern wintering grounds during June and July, and most of those taken during August, show active molt of the remiges. Of five specimens of *swainsoni*

taken in September, all had completed the replacement of their flight feathers. Wintering *ferocior* may continue the molt of the flight feathers into October, since the birds return to the breeding ground somewhat later than do *swainsoni*.

Since the more tropical *pelzelni* breeds somewhat earlier than do *swainsoni* and *ferocior*, it also commences the complete prebasic molt earlier than do those migratory forms. Molting specimens of *pelzelni* have been taken from December through May. The northern subspecies, *phaeonotus*, undergoes its annual molt at the opposite time of the year, from March through August.

Juvenals undergo a postjuvenile molt at approximately the same time as adults of the same population undergo their complete molt. Of six juvenile *swainsoni* taken on the wintering ground during April and May, only one had begun replacement of the remiges; one July specimen was midway through its wing molt, and one August specimen was completing the molt of its flight feathers. Of 10 juvenile *swainsoni* taken on the breeding grounds from late December until April 1, none had begun a molt of the juvenile flight feathers.

VOCAL CHARACTERS: The analysis of vocal characters of *M. swainsoni* is based on recordings from these samples:

M. s. swainsoni—Brazil, 12 pairs; Uruguay, three pairs

M. s. pelzelni—Brazil, three pairs; Peru, two pairs

M. s. ferocior—Argentina, 15 pairs; Bolivia, five pairs

M. s. phaeonotus—Venezuela, four pairs
Intergrades between *M. s. swainsoni* and *M. s. ferocior*—Argentina, nine pairs

Intergrades between *M. s. swainsoni* and *M. s. pelzelni*—Brazil, three pairs

Intergrades between *M. s. pelzelni* and *M. s. phaeonotus*—Surinam, four pairs

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1 and illustrated in figures 31-35.

In response to playback, or when excited by

intruding conspecifics, *M. swainsoni* vocalizes with repeated hiccups (except *ferocior*), rasps, rasp-rolls, and rolls. Most populations use a hiccup (fig. 31), which consists of two syllables of similar duration. The second syllable is accented by virtue of its much greater frequency excursion and greater amplitude. This species has two calls that have a rasping quality but that differ in their modulating frequencies. Figure 32:11 illustrates both calls, given in this instance in rapid succession by a single bird and analyzed with the narrow-band filter. The first illustrated, the rasp, is the more common of the two and does not differ from the rasp of many congeners. It normally has a modulating frequency of 75 to 95 Hertz. Less common is the rasping whistle, the second trace in figure 32:11, though I have recorded it from all subspecies. It is a sharp, whistled note that is modulated at a frequency of 40 to 50 Hertz. The rasp and rasping whistle may be delivered as isolated notes or sometimes in rapid sequence. The rasp is often used to introduce or terminate a roll, or both. The roll varies considerably in duration, frequency excursion, and in the pattern and relative amplitude of the syllables (figs. 32-34). It may be given as an isolated call, but more typically it is associated with an introductory or terminal rasp or sharp whistle. The typical pattern of the component syllables of the roll is chevron-like ("huit" note). In some populations, however, each syllable may resemble a double chevron or it may be of longer duration and approximate the trace of a sharp whistle. Rolls consisting primarily of sharp whistled notes tend to be of longer duration and to lack an introductory or terminal rasp.

Foraging birds not excited by playback or intruding conspecifics will deliver plaintive whistles (fig. 31) at intervals of several seconds. In my samples whistles vary in length from 0.2 to 0.8 second and normally were gently slurred with very little frequency excursion. Presumably these whistles serve as location notes in the communication between paired birds, for they often are given by an individual after the removal of its mate by collecting, and also in response to the termination of playback (one or two minutes after the cessation of the

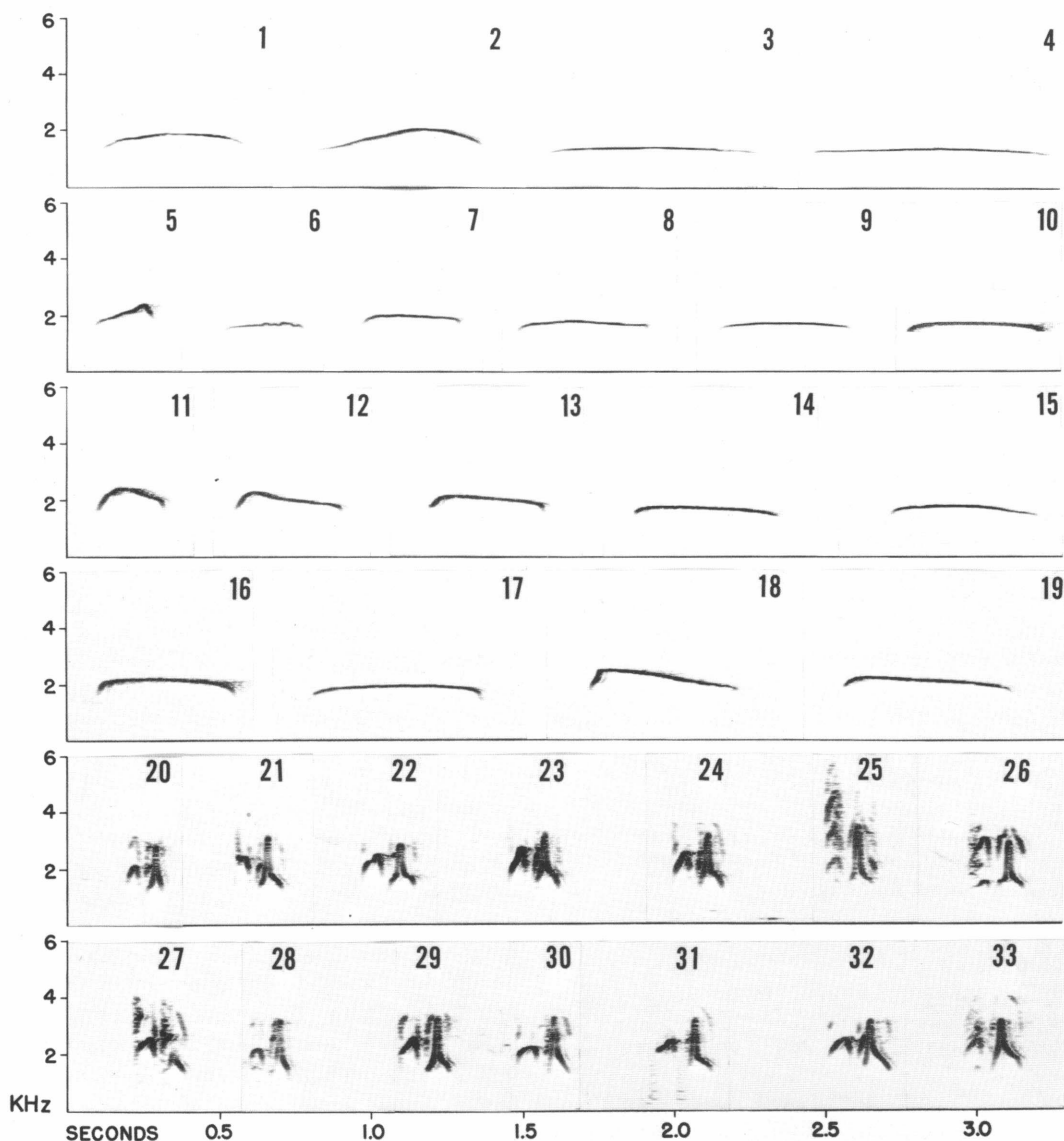


FIG. 31. Variation in vocal characters of *Myiarchus swainsoni*: whistles (1-19) and hiccups (20-33). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. s. ferocior* (Bolivia, 1, 3; Argentina, 2, 4); *M. s. swainsoni* (Brazil, 5, 7, 8, 10, 21-24; Uruguay, 6, 9, 25); *M. s. pelzelni* (Brazil, 11-14, 29; Peru, 28); *M. s. phaeonotus* (Venezuela, 18, 19, 32, 33); intergrades between *M. s. pelzelni* and *M. s. swainsoni* (Brazil, 15, 26, 27); intergrades between *M. s. pelzelni* and *M. s. phaeonotus* (Surinam, 16, 17, 30, 31); intergrades between *M. s. swainsoni* and *M. s. ferocior* (Argentina, 20).

tape recording). "Huit" notes, though regular components of the dawn song, are heard infrequently in most populations of this species during the daylight hours. Only from some

individuals of *pelzelni* did I record "huit" notes with any regularity.

DAWN SONG: Two types of dawn song have been recorded from males of *M. swainsoni*: (1)

those consisting of whistles of varying duration and extent of frequency excursion, but alternated with an occasional "huit" note (fig. 34:1, and fig. 35:1, 3, 5, 7, and 9), and (2) those

consisting of these components (whistles and "huit" notes) plus a complex phrase derived from combination of a central "huit"-like syllable and whistled notes that are modulated at

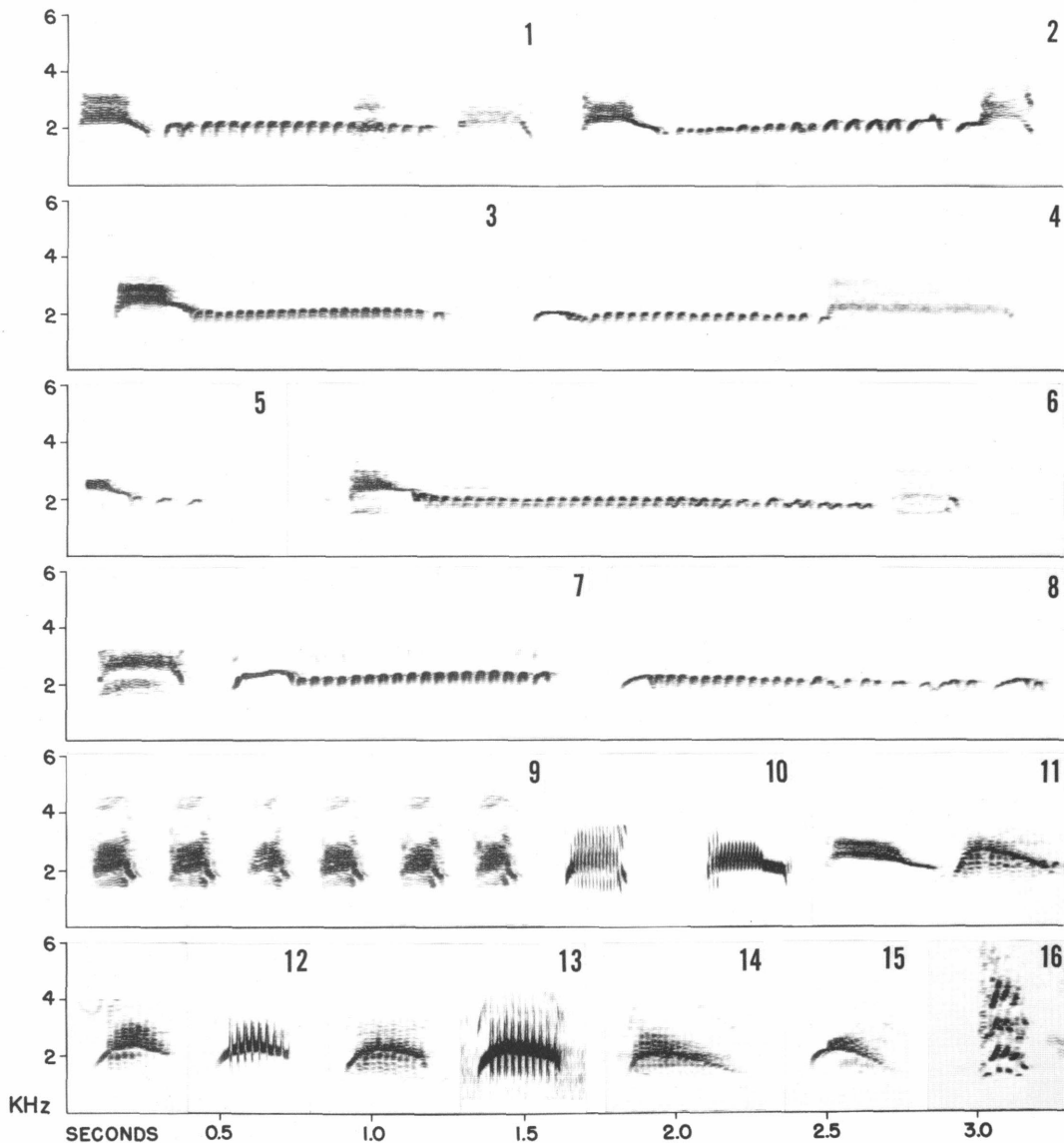


FIG. 32. Variation in vocal characters of *Myiarchus swainsoni*: rolls (1-8), rasps (1-7, 9, 10, 11 left), and rasping whistles (11 right, 12-15). Spectrograms were made from recordings of the following populations: *M. s. pelzelni* (Peru, 1, 13; Brazil, 2); *M. s. phaeonotus* (Venezuela, 5-8); *M. s. swainsoni* (Uruguay, 9; Brazil, 10, 12); *M. s. ferocior* (Argentina, 15, 16); intergrades between *M. s. phaeonotus* and *M. s. pelzelni* (Surinam, 3, 4, 11); intergrades between *M. s. swainsoni* and *M. s. ferocior* (Argentina, 14). The 300 Hz. filter was used for 10, 12b, and 13b only.

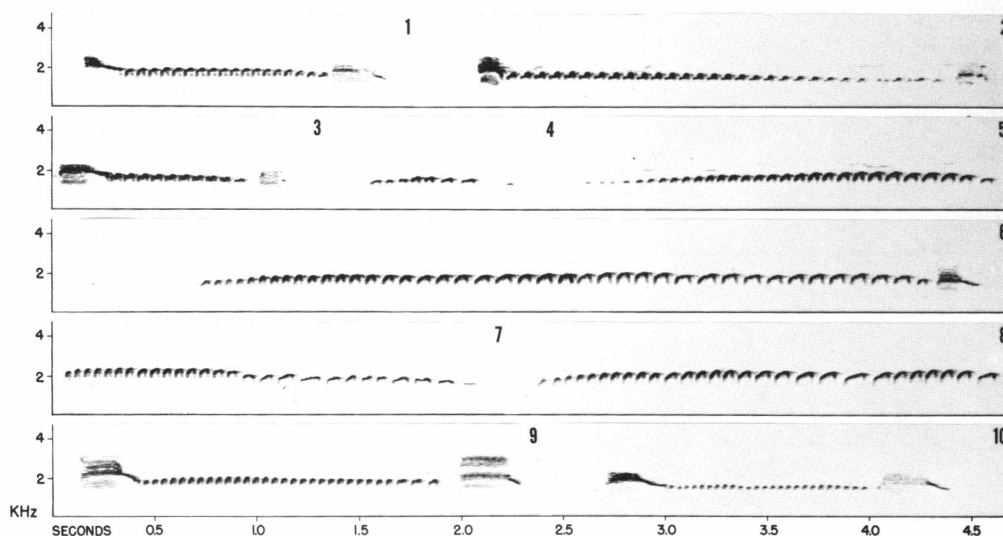


FIG. 33. Variation in vocal characters of *Myiarchus swainsoni*: rasps and rolls. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. s. ferocior* (Bolivia, 1, 7; Argentina, 2-6); intergrades between *M. s. swainsoni* and *M. s. ferocior* (Argentina, 8-10).

low to moderate frequencies (fig. 35:2, 4, 6, 8, and 10). A single male may use both types during the course of a morning's bout of dawn song, and both types were recorded at most localities where I worked. The whistles used in dawn song exhibit the same variation that one finds among whistles given during the daylight hours. The whistled note that usually introduces the complex phrase is modulated very slowly, resulting in a vibrato. The terminal component, another whistled note, is normally slurred downward in frequency and not modulated. Occasionally, however, this terminal whistle is modulated at a frequency of 40 to 50 Hertz, thus nicely demonstrating the derivation of the rasping whistle used by this species during the daylight hours.

GEOGRAPHICAL VARIATION: As in the other wide-ranging species of *Myiarchus* that exhibit substantial geographical variation in body size, there is a negative correlation between the carrier frequency and body size in *M. swainsoni*. The larger-bodied *ferocior* vocalizes at a slightly lower mean frequency than do the smaller-bodied *phaeonotus* and *pelzelni*.

Other than the variability in the carrier frequency noted above, the only significant sub-specific differentiation in vocalizations within this species is in *ferocior*, where there has been a modification of the roll and the elimination of the hiccup note from the daytime repertoire but not from the dawn song. My recordings made of 20 pairs of *ferocior* in Argentina and Bolivia contain no hiccup notes other than those contributing to the complex phrase in the dawn song. The rolls of *ferocior* may be of two types, each of which differs substantially from those of the other subspecies: (1) a series of simple, sharp whistles, each of which tends to be of longer duration than the syllables in the rolls of the other subspecies, and the roll in its entirety may be of much longer duration and be without the usual introductory and terminal rasping note (fig. 33:4-8); (2) a series of shorter syllables, each of which is a double chevron or M-shaped configuration (fig. 33:1-3).

The "huit" note, though present in the dawn song of all the subspecies, is given only infrequently during the daytime in most populations. I found it most conspicuous in the daytime

repertoire of the population of intergrades between *pelzelni* and *swainsoni* in Surinam, and in some populations of *pelzelni*.

There is a suggestion in my data that there may be geographical variation in the incidence

of the more complex phrase in the dawn song, but my samples are too small to establish this point. Of the nine *ferocior* males recorded in Argentina, eight included complex phrases in their dawn songs. In Brazil, only six of 10

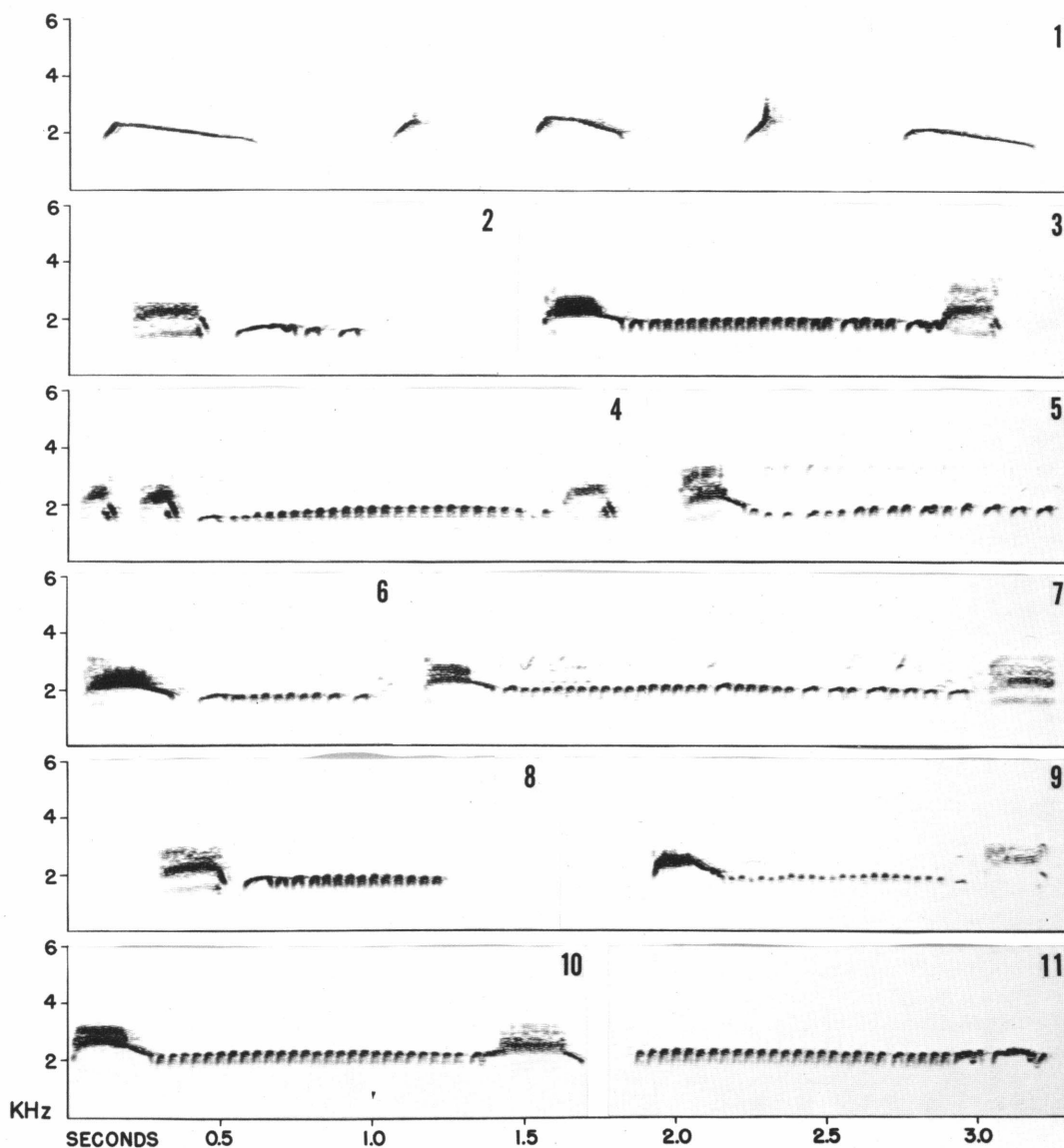


FIG. 34. Variation in vocal characters of *Myiarchus swainsoni*: dawn song (1) and rolls and rasps (2-11). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. s. phaeonotus* (Venezuela, 1); *M. s. swainsoni* (Brazil, 2, 3, 6-8; Uruguay, 4, 5); *M. s. pelzelni* (Brazil, 10, 11); intergrades between *M. s. swainsoni* and *M. s. pelzelni* (Brazil, 9).

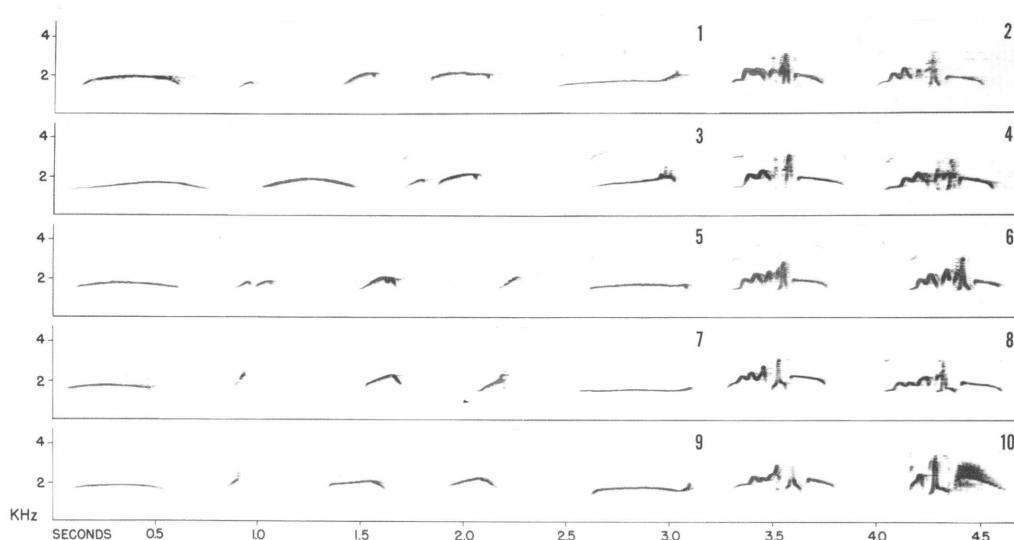


FIG. 35. Variation in vocal characters of *Myiarchus swainsoni*: dawn songs. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. s. ferocior* (Bolivia, 1, 2; Argentina, 3, 4); *M. s. swainsoni* (Brazil, 7a, b, c, 8; Uruguay, 7d, e); *M. s. pelzelni* (Brazil, 9c, d, 10a); intergrades between *M. s. swainsoni* and *M. s. ferocior* (Argentina, 5, 6); intergrades between *M. s. swainsoni* and *M. s. pelzelni* (Brazil, 9a, b, e, 10b).

swainsoni males included these phrases. Neither of the two *phaeonorhynchus* males in Venezuela used complex phrases during the period that I recorded their dawn songs (see fig. 34:1).

ITINERARY OF FIELDWORK

- 1967—November 2-19, with *ferocior* near Tucumán, Tucumán, Argentina; November 29 through December 4, with *swainsoni* at Fazenda Barreiro Rico, near Anhembi, São Paulo, Brazil; December 7, with *swainsoni* in the Sierra de Animas, Maldonado, Uruguay; December 11-14, with intergrades between *swainsoni* and *pelzelni* near Ipatinga, Minas Gerais, Brazil; December 18-21, with *pelzelni* near Salvador, Bahia, Brazil.
- 1969—April 29 through May 6, with *phaeonorhynchus* at Kavanayén, Bolívar, Venezuela.
- 1970—November 9-22, with intergrades between *swainsoni* and *ferocior* at Las Tres Marías, Corrientes, Argentina; November 23, with *ferocior* near Sáenz Peña, Chaco, Argentina; November 25-29, with *ferocior* near Tucumán again; December 2-4, on a transect across the provinces of Córdoba and Santa

Fé, Argentina, for *ferocior*; December 5-6, with intergrades between *swainsoni* and *ferocior* on a transect across the province of Entre Ríos, Argentina; December 9-14, with *swainsoni* at Fazenda Barreiro Rico again; December 18-21, with intergrades between *phaeonorhynchus* and *pelzelni* near Zanderij, Surinam.

1972—November 19-21, with *pelzelni* near Quillabamba, Cuzco, Peru.

1974—November 5-7, with *ferocior* at Villa Montes, Tarija, Bolivia.

SYSTEMATICS

Myiarchus swainsoni swainsoni Cabanis and Heine

- Myiarchus swainsoni* Cabanis and Heine, 1859, p. 72 (type locality, "Brazil"; cotypes in the Heine Collection). Hellmayr, 1927, p. 173 (in part; "types in Heine Collection examined"; synonymy). Laubman, 1940, p. 96.
- Myiarchus cantans* Pelzelni, 1868, pp. 117, 182 (in part; specimen from Paraná in the Vienna Museum, examined by Hellmayr, 1927, p. 173, and designated as a lectotype).

Myiarchus sordidus Todd, 1916, p. 96 (type locality, Carabobo, Venezuela; holotype in the Carnegie Museum, examined).

Myiarchus ferox swainsoni: Oberholser, 1918, p. 307 (new combination).

(?) *Myiarchus tyrannulus czakii* Sztolcman, 1926, p. 176 (type locality, Salto Guayra, Rio Paraná; holotype in the Warsaw Museum, not examined; presumably juvenals of *swainsoni*; see discussion on p. 602).

Myiarchus swainsoni swainsoni: Zimmer, 1938a, p. 8. Pinto, 1944, p. 170. Meyer de Schauensee, 1966, p. 351.

DIAGNOSIS: Mandible not entirely black, even in fresh specimens, but rather dark brown, becoming slightly paler proximally. (Caution: mandible of black-billed species of *Myiarchus* may pale in older museum specimens.) Outer

vane of outer rectrix only barely if at all paler than inner vane. Upperparts darker than in either *pelzelni* or *ferocior* (table 28), and tips of wing coverts and margins of tertials dull grayish brown, not broadly tipped or edged with white as in those subspecies. Underparts duller than in *pelzelni* or *ferocior*, with throat deeper gray, blending more gradually into a paler, grayish yellow abdomen.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 36): The nominate subspecies breeds from Uruguay northward through southern Brazil and extreme northeastern Argentina to southeastern Paraguay, São Paulo, and Rio de Janeiro, Brazil. It intergrades with *ferocior* in extreme western Uruguay, in the provinces of Entre Ríos and Corrientes, Argentina, and in central Paraguay (fig. 39). Intergrades with *pelzelni*

TABLE 25
Fifth Primary minus Ninth Primary (in Millimeters) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. s. swainsoni</i>					
Males	85	-1 to -8	-4.4 ± 0.16	1.45	33.32
Females	81	-1 to -8	-3.7 ± 0.17	1.50	40.42
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	22	-1 to -7	-3.9 ± 0.38	1.78	46.09
Females	13	-1 to -5	-2.8 ± 0.36	1.30	46.98
<i>M. s. ferocior</i>					
Males	51	-1 to -8	-3.6 ± 0.20	1.42	39.73
Females	21	-1 to -8	-3.3 ± 0.36	1.65	50.14
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	5	-4 to -6	-4.8 ± 0.37	0.84	17.43
Females	6	0 to -4	-2.2 ± 0.60	1.47	67.96
<i>M. s. pelzelni</i>					
Males	25	0 to -6	-3.6 ± 0.30	1.50	41.67
Females	19	-2 to -5	-3.3 ± 0.24	1.05	32.05
Intergrades between <i>pelzelni</i> and <i>phaeonotus</i>					
Males	20	0 to -6	-2.6 ± 0.31	1.39	53.53
Females	7	-1 to -5	-2.6 ± 0.48	1.27	49.49
<i>M. s. phaeonotus</i>					
Males	16	0 to -5	-2.3 ± 0.31	1.25	54.05
Females	14	+1 to -3	-1.4 ± 0.36	1.34	93.97
All Subspecies of <i>M. swainsoni</i>					
Males	224	0 to -8	-3.8 ± 0.11	1.59	42.26
Females	161	+1 to -8	-3.2 ± 0.12	1.57	48.80
Both sexes	385	+1 to -8	-3.5 ± 0.08	1.60	45.31

TABLE 26
Fourth Primary minus Tenth Primary (in Millimeters) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. s. swainsoni</i>					
Males	213	-3 to +7	+1.3 ± 0.13	1.85	137.37
Females	176	-3 to +7	+2.3 ± 0.14	1.88	82.79
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	41	-2 to +7	+1.7 ± 0.33	2.14	129.04
Females	22	0 to +6	+3.1 ± 0.38	1.80	58.14
<i>M. s. ferocior</i>					
Males	96	-2 to +6	+1.9 ± 0.17	1.71	89.77
Females	40	-1 to +6	+3.3 ± 0.25	1.58	48.65
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	8	-2 to +2	-0.1 ± 0.58	1.64	1313.60
Females	7	0 to +5	+2.9 ± 0.70	1.86	65.26
<i>M. s. pelzelni</i>					
Males	31	-4 to +7	+1.1 ± 0.37	2.05	181.13
Females	28	0 to +6	+2.4 ± 0.26	1.40	58.37
Intergrades between <i>pelzelni</i> and <i>phaeonotus</i>					
Males	24	-1 to +8	+3.2 ± 0.52	2.57	81.00
Females	10	0 to +5	+3.5 ± 0.58	1.84	52.60
<i>M. s. phaeonotus</i>					
Males	17	+1 to +7	+4.5 ± 0.47	1.94	42.84
Females	16	+3 to +8	+5.4 ± 0.36	1.46	26.84
All Subspecies of <i>M. swainsoni</i>					
Males	430	-4 to +8	1.7 ± 0.10	2.05	121.45
Females	299	-3 to +8	2.7 ± 0.11	1.92	71.12
Both sexes	729	-4 to +8	2.1 ± 0.08	2.06	97.91

have been taken in northern Paraguay and in southern Minas Gerais, Brazil, and probably occur along the Rio Paraná, Brazil, as well (fig. 37). The southernmost populations are migratory and spend the austral winter in northern South America, east of the Andes, from eastern Colombia and western Venezuela eastward and south to Paraíba, Brazil (fig. 36).

Sympatric with *M. ferox*, *M. tyrannulus*, and *M. tuberculifer* in the northern part of the range.

Specimens examined from the breeding range, 425; localities, by country, from north to south and west to east (see fig. 36; asterisks denote author's study areas): BRAZIL, Lins, São Paulo; Bebedouro, São Paulo; Bauru, São Paulo; *Fazenda Barreiro Rico, São Paulo (Anhembi); Ribeirão Fundo, São Paulo; Avaré, São Paulo; Itatiaia, Rio de Janeiro; Rio de Ja-

neiro, Rio de Janeiro; Pôrto Camargo, Paraná (Rio Paracai); Ipanema, São Paulo; São Paulo, São Paulo (Interlagos; Ipiranga; Pôrto Estrada; Emas; Salesópolis); Tibagy, Paraná (Jaguariaíva); Onça Parda, São Paulo; Corvo, Paraná; Pôrto Almeida, Paraná; Joinville, Santa Catarina; São Bento, Santa Catarina; Palmitos, Santa Catarina; Caçador, Santa Catarina; Nonohay, Rio Grande do Sul; Erebang, Rio Grande do Sul (Passo da Entrada); Vaccaria, Rio Grande do Sul (Lagôa Vermelha; Sananduva); Bom Jesus, Rio Grande do Sul; Sinimbu, Rio Grande do Sul; Uruguayana, Rio Grande do Sul; São Francisco de Paula, Rio Grande do Sul; Lagôa da Forno, Rio Grande do Sul; Santa Maria, Rio Grande do Sul; Rio Pardo, Rio Grande do Sul (San Jerônimo; Montenegro); Encruzilhada, Rio Grande do Sul; São Lourenço, Rio Grande do Sul; Bagé, Rio

TABLE 27
Body Weight (in Grams) in Samples of *Myiarchus swainsoni*

Sample	N	Range	Mean, S.E.	S.D.	S.V.
<i>M. s. swainsoni</i>					
Males	42	21.5 - 28.5	25.03 ± 0.61	3.92	15.68
Females	28	21.3 - 28.9	25.19 ± 0.42	2.22	8.82
Intergrades between <i>swainsoni</i> and <i>ferocior</i>					
Males	10	23.0 - 29.5	27.39 ± 0.61	1.93	7.06
Females	2	—	29.00 —	—	—
<i>M. s. ferocior</i>					
Males	8	27.5 - 33.5	30.63 ± 0.71	2.00	6.52
Females	3	—	25.33 —	—	—
Intergrades between <i>swainsoni</i> and <i>pelzelni</i>					
Males	0	—	— —	—	—
Females	0	—	— —	—	—
<i>M. s. pelzelni</i>					
Males	1	—	24.00 —	—	—
Females	2	—	21.00 —	—	—
Intergrades between <i>pelzelni</i> and <i>phaeonorotus</i>					
Males	4	—	25.38 —	—	—
Females	1	—	23.00 —	—	—
<i>M. s. phaeonorotus</i>					
Males	2	—	24.00 —	—	—
Females	4	—	21.75 —	—	—

Grande do Sul. PARAGUAY, Caaguazú, Yhú (Colonia Independencia). ARGENTINA, Iguazú, Misiones (Puerto Bossetti; Arroyo Uruguay-i); Tobuna, Misiones; Eldorado, Misiones (Puerto Piray); Santa Ana, Misiones (Bonpland; San Ignacio); Ituzaingó, Corrientes; Azara, Misiones (Concepcion; Playadito, Corrientes); Santo Tomé, Corrientes. URUGUAY, Arroyo Cuaró, Artigas (Arroyo Tres Cruces); Arroyo

de la Invernada, Artigas; Laureles, Tacuarembó; Cerro Largo, Rivera (Paso Mazangano; Río Negro); Quebrada de los Cuervos, Treinta y Tres; Mansavillagra, Florida; Pirarajá, Lavalleja (Río Cebollati); Castillos, Rocha; Arroyo del Tigre, San José (Arazati); *Sierra de Animas, Maldonado (Minas, Lavalleja); Garzón, Rocha.

Migrant and wintering specimens examined, 81; localities, by country, from north to south and west to east (see fig. 36): TRINIDAD. VENEZUELA, San Antonio del Golfo, Sucre; El Trompillo, Carabobo; Acarigua, Portuguesa; Altigracia de Orituco, Guárico; Maturín, Monagas; El Baúl, Cojedes; Palenque, Guárico; Santa María de Ipire, Guárico; Ciudad Bolívar, Bolívar; Caicara, Bolívar; El Dorado, Bolívar; Puerto Ayacucho, Amazonas; Santa Teresa de Uairén, Bolívar; Las Carmelitas, Amazonas; Boca del Río Ocamo, Amazonas; Buena Vista, Amazonas (Solano). GUYANA, Georgetown; Annai. COLOMBIA, La Herrera, Cundinamarca; Puerto Venecia, Caquetá. BRAZIL, Frechal, Rio Branco; Rio Mucajá, Rio Branco;

TABLE 28
Reflectance Characteristics of the Back in
Samples of the Four Subspecies of
Myiarchus swainsoni

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>phaeonorotus</i>	11	5.22	0.44	Standard	
<i>swainsoni</i>	13	8.08	0.65	17.1	17.5
<i>ferocior</i>	18	9.48	0.76	25.4	26.0
<i>pelzelni</i>	9	9.83	0.74	27.5	28.1



FIG. 36. Distribution of *Myiarchus swainsoni swainsoni*. Breeding range is indicated by localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). Triangles represent localities where migrant and wintering specimens have been taken. See page 514 for lists of these localities and page 512 for an itinerary of author's fieldwork with this taxon.

Yucabi, Amazonas; Benevides, Pará; Santarém, Pará (Rio Tapajóz); Manáos, Amazonas; Caxiricatuba, Pará; São Bento, Maranhão; Ipú,

Ceará; Curemas, Paraíba. BOLIVIA, Tirague, Cochabamba; Tucavaca, Santa Cruz. PARAGUAY, Orloff, Chaco.

Myiarchus swainsoni pelzelni Berlepsch

Myiarchus pelzelni Berlepsch, 1883, p. 139 (type locality "Bahia"; holotype in the Senckenberg Museum). Berlepsch, 1907, p. 477. Todd, 1922, p. 193 (in part).

Myiarchus pelzelni pelzelni: Hellmayr, 1925b, p. 19; 1927, p. 171 (synonymy; "type in Berlepsch Collection examined"). Pinto, 1936, p. 120. Laubman, 1940, p. 96. Mees, 1968, p. 104.

Myiarchus swainsoni pelzelni: Zimmer, 1938a, p. 3 (new combination). Pinto, 1944, p. 169. Gyldenstolpe, 1945a, p. 206. Meyer de Schauensee, 1966, p. 351.

DIAGNOSIS: Mandible not entirely black, even in fresh specimens, but rather light to dark brown, becoming slightly paler proximally. (Caution: mandible of black-billed species may pale in older museum specimens.) Outer vane of outer rectrix somewhat paler than rest of tail. In fresh plumage only, rectrices and upper tail coverts conspicuously fringed with Antique Brown. Upperparts as in *ferocior*, but paler than in other subspecies (table 28). Abdomen richer yellow and wing coverts more broadly tipped with white than in *swainsoni*. Separable from *ferocior* by smaller size and lack of contrasting darker auricular area.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 37): This is the race of the southern and eastern perimeter of the Amazon basin, south to Minas Gerais, southern Goiás and Mato Grosso, and westward through northern Bolivia to southeastern Peru. I concur with Zimmer (1938a) that the specimen (AMNH 116690) from southeastern Colombia, referred to *pelzelni* by Todd (1922) and Hellmayr (1927), is best considered a wintering individual of *ferocior*. Intergrades with *phaeonorotus* over an extensive region including eastern Guyana, Surinam, along the Amazon from the delta region westward to Manaus, and along the lower Rio Negro and Rio Branco, Brazil (fig. 37; discussed in detail, p. 531). Intergrades with *swainsoni* in northern Paraguay and in southern Minas Gerais, and probably also along the Rio Paraná, Brazil (fig. 37). Presumably intergrades with *ferocior* in central Bolivia, but the lack of suitable material from Bolivia and the problem of identifying intergrades between forms that differ mainly in size make it difficult to deter-

mine if, in fact, the breeding ranges of the two forms come together. Nonmigratory.

Sympatric with *M. ferox*, *M. tuberculifer*, and *M. tyrannulus* throughout much of its range.

Specimens examined, 66; localities, by country, from north to south and west to east (see fig. 37; asterisks denote author's study areas): BRAZIL, Mexiana, Pará (Ilha de Marajó); Tapará, Pará; São Bento, Maranhão; Speé, Ceará; Baturité, Ceará; Therezina, Piauí; Amarante, Piauí; Iguatu, Ceará; Floriano, Piauí; Alto Parnaíba, Maranhão; Cachimbo, Pará; Juazeiro, Baía; Jacaré, Mato Grosso (Alto Xingú); Villa Nova, Baía; Serra do Roncador, Mato Grosso; *Salvador, Baía (Madre de Deus); Giguí, Baía; Rio das Almas, Goiás; Chapada, Mato Grosso; Aragarcas, Goiás (Rio Araguaia); Goiânia, Goiás; Urucum, Mato Grosso (Corumbá). PERU, *Quillabamba, Cuzco (Chauillay). BOLIVIA, La Horquilla, El Beni; Trinidad, El Beni; Buena Vista, Santa Cruz.

RELATIONSHIP OF
pelzelni WITH *Myiarchus swainsoni*

Earlier workers generally regarded *pelzelni* as being specifically distinct from *swainsoni*, though recognizing that the two forms are closer to each other than either is to *M. ferox*. Todd (1922, p. 196), unaware that the northern specimens of *swainsoni* were actually migrants from the south, was impressed with the apparent extensive overlap in the ranges of the two forms: "As this extensive range [of *swainsoni*] embraces territory in which *M. pelzelni* is also found, they must be distinct species, although related." Hellmayr (1927, p. 171) said: "*Myiarchus pelzelni* Berlepsch is now universally admitted to be a perfectly distinct species, and its characters having been clearly defined by Berlepsch, Todd and myself need not be insisted upon."

Zimmer (1938a), who was the first to regard *pelzelni* as conspecific with *swainsoni*, wrote, "I can find no sharp line of demarcation between *pelzelni* and *swainsoni* sufficient to justify the maintenance of specific separation . . . Intergradation between the two forms appears to take place in Paraguay. Specimens from east

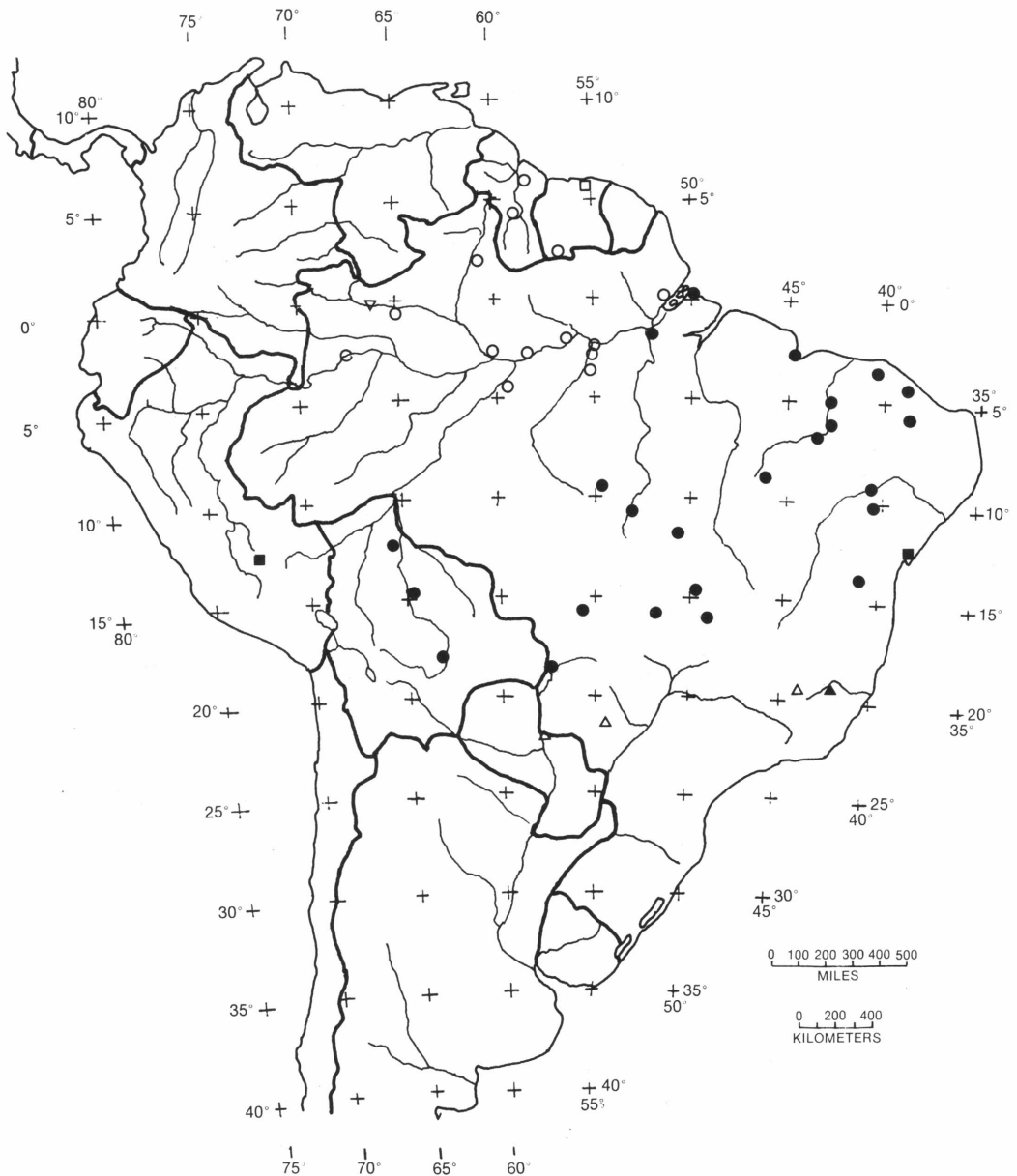


FIG. 37. Distribution of *Myiarchus swainsoni pelzelni* as indicated by localities of specimens examined (solid circles) and of sites where author studied this taxon in the field (solid squares). A zone of intergradation between *M. s. pelzelni* and *M. s. swainsoni* is suggested by localities of specimens examined (open triangles) and by site where author studied an intermediate population (solid triangle). A zone of intergradation between *M. s. pelzelni* and *M. s. phaeonotus* is suggested by localities of specimens examined (open circles) and of site where author studied an intermediate population (open square). Specimen taken at the locality in northwestern Brazil, marked by inverted open triangle, is thought to be a wintering intergrade between *M. s. pelzelni* and *M. s. swainsoni*. See pages 517 and 534 for lists of these localities and page 512 for an itinerary of author's fieldwork with these taxa.

of Caaguassú and east of Villa Rica are rather typical *swainsoni*, but a skin from Colonia Risso and another without definite locality, are a little paler on the upperparts than the average and have more prominent pale wing-bars. None of the Paraguayan specimens are near the maximum of *swainsoni* in dimensions although they come within the range of variations of both *swainsoni* and *pelzelni*." Most recent workers have followed Zimmer (Pinto, 1944; Gyldenstolpe, 1945a; Meyer de Schauensee, 1966). Todd, however, remained dissatisfied with this treatment, and in a letter to Zimmer dated April 3, 1951, wrote: "I agree with you that my *Myiarchus 'sordidus'* merely represents winter migrants from beyond the Equator, but I cannot quite follow you in making *swainsoni* and *pelzelni* conspecific." Mees (1968) likewise concluded that there was no evidence for intergradation and treated *pelzelni* and *swainsoni* as distinct species.

Intergradation between *swainsoni* and *pelzelni* occurs in southern Minas Gerais, Brazil, and probably along the Rio Paraná, although I have seen no specimens from that contact zone. There are three specimens in São Paulo (MZSP 25196-25198), collected in southern Minas Gerais, that have the longer wing of *swainsoni* but are intermediate between *swainsoni* and *pelzelni* in coloration; Pinto (1944) assigned them to *pelzelni*. I took a series of breeding birds from the same general area in 1967 (AMNH 822037-822040). These are also closer to *swainsoni* in size but, even in worn plumage, are recognizably intermediate in plumage coloration as illustrated by comparative reflectance characteristics of the back (table 29). That intergradation between *pelzelni* and *swainsoni* also occurs in northern Paraguay is suggested by a specimen (AMNH 497247) from Colonia Risso, Paraguay. Zimmer's remarks (1938a) on this specimen, as well as on another simply labeled "Paraguay" (AMNH 497246), are quoted above, and I agree that both should be regarded as intermediate between *pelzelni* and *swainsoni*.

I was unable to detect any differences between the vocal characters of *pelzelni* and *swainsoni* (p. 510). Territorial *pelzelni* were easily located in Baía, Brazil, and in the

Urubamba valley of Peru, because they responded positively to a reconnaissance tape made from nominate *swainsoni* in São Paulo, Brazil. I tested a pair of *pelzelni* at Quillabamba, Cuzco, Peru, on November 20, 1972, and found them to be responsive to *swainsoni* playback tape:

Experiment 8—study area 14 km. S of Quillabamba. Tapes used, Tucumán *ferocior* vs. *M. ferox*. Location of birds unknown at start. Heard none calling while I set up experiment. Start at 6:10 A.M. One bird showed at 6:12, calling well, about 50 ft. from *ferocior* model. Both birds there at 6:12:30, giving rolls and hiccups. Still at same distance at 6:14. Three *pelzelni* at same spot at 6:15, giving rasps, rolls, and hiccups. Interactions between the three, at 50 ft. from *ferocior* model. Moved out to 70 ft., then to 100 ft. at 6:16, at cable switch. Still out of experimental area at 6:19. In to 60 ft. of new *ferocior* model at 6:20. In to 40 ft. of model at 6:21. Occasional roll and hiccup, now, but no sustained calling as before. Still out at 40 ft. at 6:23. A very weak, unsustained response.

Experiment 9—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. Birds silent, location unknown at start at 6:28 A.M. Birds started calling at once, and appeared about 60 ft. from *swainsoni* model. Three birds at 50 ft. at 6:30, calling excitedly (rolls, rasps, and hiccups). One had moved into 15 ft. of *swainsoni* model by 6:31, calling well. Back out to 50 ft. Still there, calling well, at cable switch at 6:35. One moved to 60 ft. of new *swainsoni* model within 30 seconds. In to 15 ft. of new *swainsoni* model at 6:37. In to 10 ft., calling well. Back out to 30 ft. at

TABLE 29
Reflectance Characteristics of the Back in
Samples of *swainsoni* and *pelzelni* and of
Intergrades from the Zone of Contact^a

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>swainsoni</i>	13	8.08	0.65	Standard	
Intergrades	4	8.77	0.72	3.2	4.9
<i>pelzelni</i>	9	9.83	0.74	8.1	8.3

^aFrom Ipatinga, Minas Gerais, Brazil (solid triangle in fig. 37).

6:39. Calling excitedly at 30 ft. from *swainsoni* model at 6:40. All three birds at 30 ft. from *swainsoni* model at 6:41. Two had moved out to midpoint by end of experiment. Good response, including reorientation, toward *swainsoni* playback tape!

The only other set of playback experiments relevant to the relationship of *pelzelni* with *M. swainsoni* is that conducted with a pair of birds on the Hannover savanna, near Zanderij, Surinam; these birds are morphological intergrades between *pelzelni* and *phaeonotus*. This pair also were very responsive to the *swainsoni* playback tape. The following field notes were made on December 21, 1970:

Experiment 69—Tapes used, São Paulo *swainsoni* vs. *M. tuberculifer*. Birds silent, location unknown at start at 8:58 A.M. Birds began calling outside the experimental area at once. Still giving rolls outside the area at 9:03. One appeared 20 ft. from *swainsoni* model at 9:03:30, giving rasps and rolls. To 5 ft. of model at 9:04. Both birds within 8 ft. of *swainsoni* model at 9:04:30. Both within 10 ft. of model at cable switch at 9:05. Both out to 20 ft. within 30 seconds. Had moved out to 30 ft. by 9:07. One moved over to new *swainsoni* area at 9:09:30, to within 25 ft. of model; then to 15 ft. of model at 9:11. Other bird left experimental area just before end of experiment. Fair response and reorientation toward *swainsoni* playback tape.

Experiment 70—same locality, pair, and date as above. Tapes used, *M. ferox* vs. *M. tuberculifer atriceps*. Birds silent at start, out of experimental area. Start at 9:15 A.M. Birds began calling outside area at 9:19, but then called only briefly. Gave occasional rasp and roll from same locality for next few minutes. Discontinued experiment after seven minutes—no response at all.

Experiment 71—same locality, pair, and date as above. Tapes used, *M. ferox* vs. *M. t. tuberculifer*. Birds silent, at start, apparently outside experimental area. Start at 9:28 A.M. Birds calling outside area at 9:30 (100 ft. from *tuberculifer* model; can see them clearly). Then became silent and inconspicuous, except for a brief encounter with another tyrannid. Gave one hiccup call at 9:34. Occasional rasp and roll. A pair of *M. ferox* showed in the *ferox* area at 9:34:30. The *ferox* moved to within 15 ft. of *ferox* model by time of cable switch. Discontinued experiment at this point—no response from these intergrades!

Experiment 72—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. *M.*

ferox. Birds silent, location unknown at start at 9:38 A.M. Birds began giving rasps and rolls about 100 ft. out, right after start. Pair of intergrades had moved to within 20 ft. of *swainsoni* model by 9:40. One *ferox* appeared at midpoint. Both intergrades within 15 ft. of *swainsoni* model, and *ferox* moved over into *ferox* area. Intergrades much more vocal than in last two experiments. Intergrades crisscrossing *swainsoni* model, giving rasps and rolls. Another crisscross. Both within 12 ft. of *swainsoni* model at 9:43. The *ferox* is within 5 ft. of *ferox* model. Both intergrades within 10 ft. of *swainsoni* model at time of cable switch at 9:45. One intergrade moved to 30 ft. of new *swainsoni* model within 1 minute. The *ferox* reoriented to new *ferox* area by 9:48. Both intergrades at 30 ft. from *swainsoni* model at 9:48:30. The *ferox* is only 2 ft. from *ferox* model at 9:49. Intergrades calling well at 30 ft. from *swainsoni* model; crisscrossed *swainsoni* area at 9:50. The *ferox* is giving hiccups and rattles near *ferox* model. Intergrades remained within 30 ft. of *swainsoni* model for rest of experiment, calling well. Strong response, including orientation, of intergrades between *pelzelni* and *phaeonotus* to *swainsoni* playback tape!

Specimens of intergrades between *pelzelni* and *swainsoni* examined, 15; localities, by country, from north to south and west to east (see fig. 37; asterisk denotes author's study area): BRAZIL, San José da Lagôa, Minas Gerais (Lagôa Santa); *Ipatinga, Minas Gerais (Rio Doce); Vaccaria, Mato Grosso. PARAGUAY, Colonia Risso.

Wintering specimens examined, 1; locality: BRAZIL, Yucabi, Amazonas.

Myiarchus swainsoni ferocior Cabanis

Myiarchus ferocior Cabanis, 1883, p. 214 (type locality, San Javier, Tucumán, Argentina; holotype in the Berlin Museum).

Myiarchus ferox ferocior: Berlepsch, 1907, p. 477 (new combination). Hartert and Venturi, 1909, p. 203. Oberholser, 1918, p. 307.

Myiarchus (?) *fortirostris* Todd, 1913, p. 171 (type locality, Sara, Bolivia; holotype in the Carnegie Museum, examined).

Myiarchus pelzelni: Todd, 1922, p. 193 (in part). Wetmore, 1926, p. 336.

Myiarchus pelzelni ferocior: Hellmayr, 1925b, p. 18 (new combination); 1927, p. 172 (synonymy).

Myiarchus swainsoni ferocior: Zimmer, 1938a, p. 5 (new combination). Steinbacher, 1962, p. 77. Olrog, 1963, p. 256. Meyer de Schauensee, 1966, p. 351.

DIAGNOSIS: Mandible quite pale throughout (not dark brown or black). Outer vane of outer rectrix noticeably paler than inner vane. Upperparts pale, as in *pelzelni* (table 28), but throat less white and abdomen less yellow than in that form. Auriculars conspicuously darker than surrounding plumage. Tips of wing coverts and edges of tertials white or yellowish white, as in *pelzelni*. The largest subspecies (see tables 22 and 23).

The hiccup note is absent from the vocal response to intruding conspecifics and the repeated rolls often are of longer duration and without the usual introductory and terminal rasping notes that characterize the other subspecies.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 38): Breeds from the Argentine provinces of Buenos Aires and La Pampa northward through most of Argentina, western Paraguay, and southeastern Bolivia. The range of this subspecies corresponds closely to the South American chaco (Short, 1975, p. 168). Intergrades with *swainsoni* in extreme western Uruguay, eastern Argentina, and central Paraguay, and presumably with *pelzelni* in central Bolivia (fig. 39). The southernmost populations are migratory, and winter in the western perimeter of the Amazon basin as far north as southern Colombia (fig. 38).

Migrants and wintering individuals are known to frequent habitats far more mesic than those preferred for breeding. John Fitzpatrick (personal commun.) has observed *ferocior* in the primary tropical Amazonian forest of Madre de Dios, Peru, where it tends to be silent and remain high in the canopy, quite unlike its habits in the chaco of Bolivia and Argentina. Likewise, J. V. Remsen, Jr., has taken wintering *ferocior* in the Amazonian forest near Leticia, Amazonas, Colombia (MVZ 165047).

Sympatric with *M. tyrannulus* throughout all of its range, and parapatric with *M. tuberculifer* at the base of the Andes.

Specimens examined from the breeding range, 118; localities, by country, from north to south and west to east (see fig. 38; asterisks denote author's study areas): BOLIVIA, Lagunillas, Santa Cruz (Gutiérrez; Montegudo, and Tomina, Chuquisaca); *Villa Montes, Tarija. ARGENTINA, Aguaray, Salta;

Orán, Salta (Urundel; Miraflores; Yuto, Jujuy); Anta, Salta (Río del Valle); Trancas, Tucumán; Pampa de los Guanacos, Chaco; Río Bermejo, Chaco; *Tucumán, Tucumán (Tapia; El Saladillo; San Pablo; El Timbó); *Sáenz Peña, Chaco; Concepción, Tucumán (Leales; Río Colorado; La Cocha); Andalgalá, Cajamarca; Ocampo, Santa Fé; Frías, Santiago del Estero; Tostado, Santa Fé; Santa Elena, Entre Ríos (Maciá); Potreo de Garay, Córdoba; *El Tío, Córdoba; *Santa Fé, Santa Fé (Pueblo Brugo); Embalse, Córdoba; Piedra Blanca, San Luis (Santa Rosa); Tigre, Buenos Aires; La Plata, Buenos Aires (Barracas al Sud; Los Talos); Victorica, La Pampa (Conhelo; Luán Toro).

Migrant and wintering specimens examined, 28; localities, by country, from north to south and west to east (see fig. 38): COLOMBIA, Florencia, Caquetá; Leticia, Amazonas. EC-UADOR, Limoncocha, Napo. PERU, Iquitos, Loreto; Shapaja, San Martín; Pucallpa, Loreto; Boca de Río Colorado, Madre de Dios. BOLIVIA, Susi, El Beni; Huanay, La Paz; Todos Santos, Cochabamba; Buena Vista, Santa Cruz (Río Surutú; Sara; Andrés Ibáñez); Comarapa, Santa Cruz. BRAZIL, João Pessoa, Amazonas.

RELATIONSHIP OF

ferocior WITH *Myiarchus swainsoni*

The differences in size, plumage coloration, and vocal characters between *ferocior* and other forms of *M. swainsoni* are sufficient to give the matter of their relationship special attention. It was Zimmer (1938a) who first proposed that *ferocior* should be allied with *M. swainsoni*. He lacked adequate material with which to demonstrate intergradation between *ferocior* and *swainsoni* but he presumed that it occurred in Uruguay and possibly elsewhere. Most authors have followed Zimmer.

INTERPRETATION AND SIGNIFICANCE OF PLAYBACK EXPERIMENTS

Because my South American fieldwork began in northwestern Argentina, I acquired experience with *ferocior* before becoming familiar with any other population of *M. swainsoni*. I had no difficulty assembling a playback tape of the repertoire of *ferocior* because this

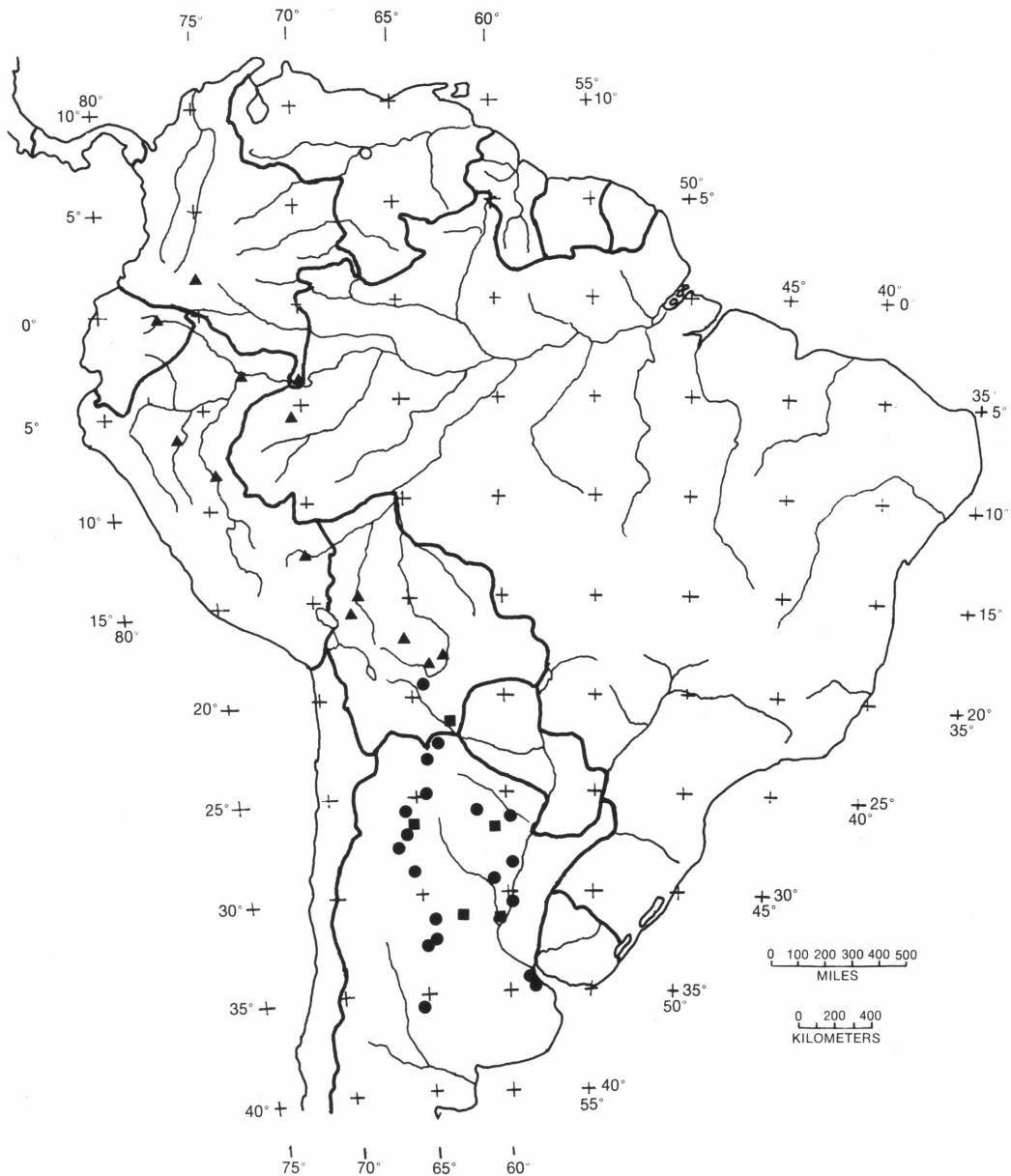


FIG. 38. Distribution of *Myiarchus swainsoni ferocior*. Breeding range is indicated by localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). Solid triangles represent localities where migrant and wintering individuals have been taken. Specimen taken in Venezuela, marked by an open circle, is thought to be a wintering intergrade between *M. s. ferocior* and *M. s. swainsoni*. See page 521 for lists of these localities and page 512 for an itinerary of author's fieldwork with this taxon.

form is abundant in the chaco of Tucumán. My next field station was in São Paulo, Brazil, where I found nominate *swainsoni* equally

common but quite unresponsive to playback of Tucumán *ferocior*. This lack of response did not surprise me because I noticed obvious dif-

ferences between the repertoires of *ferocior* and nominate *swainsoni* in the field, even before I had had an opportunity to analyze them spectrographically. On the basis of these differences in vocal characters and the appreciable morphological differences, and without the benefit of experience I later acquired in the field with other populations, I was tempted to question Zimmer's conspecific treatment.

During my fieldwork in São Paulo in 1967, and on a return trip in 1970, I conducted 23 playback experiments with eight territorial pairs of nominate *swainsoni*. The playback tapes tested in these experiments were of São Paulo *swainsoni*, Tucumán *ferocior*, *M. tyrannulus*, *M. ferox*, and of four West Indian species of *Myiarchus* (*stolidus*, *nugator*, *barbirostris*, and *oberi*). The only consistently positive response was to the playback of São Paulo *swainsoni*. The following field notes, made on December 3, 1967, illustrate this discriminatory ability of nominate *swainsoni* in São Paulo:

Experiment 59—study area along new road, Fazenda Barreiro Rico. Tapes used, Tucumán *ferocior* vs. *M. stolidus*. Pair of *swainsoni* calling sporadically outside experimental area at start of experiment. Start at 3:20 P.M. No response. Cable switch at 3:27. Saw three *swainsoni* foraging outside of experimental area during first half of experiment, and occasionally vocalizing. Stopped experiment due to lack of response.

Experiment 60—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. Tucumán *ferocior*. Start at 3:30 P.M. One *swainsoni* appeared at 3:31:30, 40 ft. from *swainsoni* model. A pair of *swainsoni* are 30 ft. from *swainsoni* model at 3:32. One flew over to *ferocior* area, perched 20 ft. above *ferocior* model; joined by a second bird, but in 40 seconds, both had moved out of the area. Back into *swainsoni* area at 3:34, 40 ft. from the model. One moved to perch 12 ft. from *swainsoni* model just before cable switch at 3:37. Within 30 seconds, the one bird reoriented to new *swainsoni* area, 40 ft. from the model. Calling hiccups and rolls. One moved to 10 ft. at 3:38, in a study; crisscross, perch at 8 ft. from model. Calling excitedly about 40 ft. from *swainsoni* model. One *swainsoni* attacked the *swainsoni* model at 3:43, then perched 8 ft. from the model, in a study. Calling excitedly. Both *swainsoni* in a radius of 15 ft. of *swainsoni* model at 3:44, at end of experiment. Good, strong response, including reorientation, to *swainsoni*; no response to *ferocior*.

Here are my field notes made on a series of experiments with another pair of nominate *swainsoni* in São Paulo, on December 10, 1970:

Experiment 66—study area along edge of woods, Fazenda Barreiro Rico. Tapes used, São Paulo *swainsoni* vs. *ferocior*. No birds calling in area at start of experiment at 5:18 P.M. Heard *swainsoni* within 30 seconds, out of area. One showed in *swainsoni* area by 5:21. Both birds there by 5:22, calling excitedly. Crisscross of *swainsoni* model at 5:24. Both calling well in *swainsoni* area at cable switch at 5:25. Both *swainsoni* reoriented to new *swainsoni* area within 1 minute. Calling within 30 to 40 ft. radius of new *swainsoni* model throughout second half of experiment.

Experiment 67—same locality, pair, and date as

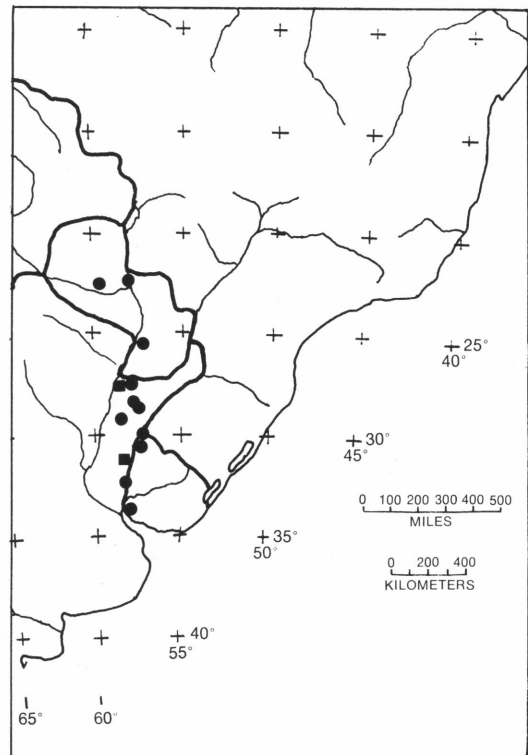


FIG. 39. A zone of intergradation between *Myiarchus swainsoni swainsoni* and *M. s. ferocior* as suggested by localities of specimens examined (circles) and by sites where author studied intermediate populations (squares). See page 529 for a list of these localities and page 512 for an itinerary of author's fieldwork with these populations.

above. Tapes used, *M. ferox* vs. Tucumán *ferocior* (to determine stimulus value of *ferocior* tape with a pair already stimulated by *swainsoni* tape). Pair of *swainsoni* silent for several minutes prior to start at 5:45 P.M. At 5:47, a *swainsoni* could be heard hiccuping outside the experimental area. Can be seen foraging about 300 ft. away! No response to *ferocior*. At 5:30, one *M. ferox* appeared in the *ferox* area and made a pass at the *ferox* model (this was first indication of *M. ferox* present in this particular study area). Cable switch at 5:52, and the *M. ferox* reoriented at once. It gave a roll directly over the *ferox* model. Another pass at 5:54. Repeated crisscrossing of *ferox* model by the single *M. ferox*. A *swainsoni* appeared in the *ferocior* area at 5:56, giving hiccups, but stayed out at a radius of 40 ft. No direct orientation toward *ferocior* model. The *M. ferox* in another pass at *ferox* model at 5:58. In a study at 6 ft. from *ferox* model. The *swainsoni* had moved out of the area, still hiccupping.

Experiment 68—same locality, pair, and date as above. Tapes used, *M. ferox* vs. São Paulo *swainsoni*. Start at 6:03. Heard a *ferox* roll within *ferox* area within 1 minute. A *swainsoni* giving hiccups and rolls in *swainsoni* area by 6:04:30. Pair of *swainsoni* within 30 ft. of *swainsoni* model at 6:05. Calling excitedly at radius of 20 to 40 ft. from *swainsoni* model, until cable switch at 6:10. Pair of *swainsoni* reoriented to new *swainsoni* area, calling excitedly, 30 ft. from new model at 6:14. Both within 15 feet at 6:15, calling excitedly. Remained there until end of experiment. No further notes taken on the response of *M. ferox*, which reoriented to new *ferox* area as expected. Strong response to *swainsoni*, including reorientation; no response to *ferocior*.

In 1970 I returned to Tucumán and conducted the reciprocal set of experiments, i.e., tests of the responsiveness of *ferocior* to the playback of São Paulo *swainsoni*. Fourteen experiments were run with four pairs of territorial *ferocior*, using playback tapes of Tucumán *ferocior*, São Paulo *swainsoni*, *M. ferox*, *M. tyrannulus*, and Tucumán *atriceps*. All four pairs of *ferocior* were able to discriminate between these tapes, and none responded to any tape other than Tucumán *ferocior*. The following field notes, made on November 29, 1970, illustrate this discriminatory ability of *ferocior* in Tucumán:

Experiment 19—study area two, along Río Tapia. Tapes used, *M. ferox* vs. São Paulo *swainsoni*. No

birds calling at start, location unknown. Start at 7:07 A.M. Had to discontinue momentarily as a noisy train passed. No show of any birds by the cable switch at 7:15. At 7:16 a pair of *ferocior* passed through the new *swainsoni* area; they gave one roll, then continued on out of the area. No response. At 7:21, heard *ferocior* giving rolls outside of experimental area. Giving whistles outside area at end of experiment. No response at all to *swainsoni* tape!

Experiment 20—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. *atriceps*. The pair had moved well out of area, giving plaintive whistles. Start at 7:25 A.M. One *ferocior* showed in *atriceps* area in 30 seconds. Gave a roll. Moved over to *ferocior* area at 7:26:30, within 5 ft. of model. Giving rolls. To 4 ft. of *ferocior* model at 7:28, calling well. In a study at 4 ft. Out to 40 ft. briefly, then back to 6 ft. of *ferocior* model. Giving rolls at 10 ft. at 7:30. In to 5 ft. of model. Giving rolls in study at 3 ft. of *ferocior* model at cable switch at 7:32. Moved out to 20 ft. of new *atriceps* model. Over to new *ferocior* area by 7:33. Within 20 ft., giving rolls. To 10 ft. of new *ferocior* model at 7:35. Study at 6 ft. A second *ferocior* showed at 7:36. Both birds within 15 ft. of *ferocior* model, one gave a pass at 7:37. Good example of consistent response, including reorientation, to *ferocior* tape. Both birds still calling well near *ferocior* model at end of experiment.

Experiment 21—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. Pair of *ferocior* dropped back out of experimental area shortly after the last experiment. Start at 7:44 A.M. Can see one *ferocior* foraging about 150 ft. away. Giving whistles. No response to *swainsoni* tape during 7 minutes of playback, though I can hear one whistling outside the experimental area. Discontinued the experiment at the halfway point.

Experiment 22—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. São Paulo *swainsoni*. Pair silent, location unknown. Start at 7:54 A.M. One showed at midpoint at 7:57, then went directly to *ferocior* model, giving rasping notes and rolls. In a study at 5 ft. from *ferocior* model, then at 3 ft. To another perch at 3 ft. giving rolls. Pass at the model at 7:59. Crisscross of *ferocior* model. In a study at 3 ft. at 8:00. Pass at 8:00:30. Sat on same branch as the model, 1 ft. away, at cable switch at 8:01. Out to 15 ft. in 30 seconds. A second *ferocior* appeared in new *ferocior* area at 8:02, calling about 30 ft. from the new *ferocior* model. The first bird moved to midpoint at 8:03. Over to new *ferocior* area at 8:03:30. Both birds in

new *ferocior* area when I collected one at end of experiment. Good, strong response to *ferocior*, and lack of response to *swainsoni*.

Playback experiments with *ferocior* in the chaco of southern Bolivia in 1974 revealed the same lack of response to playback of São Paulo *swainsoni*. I conducted six experiments with three territorial pairs of *ferocior*, using the following tapes: Tucumán *ferocior*, São Paulo *swainsoni*, *M. tyrannulus*, *M. ferox*, Tucumán *atriceps*, and Venezuelan *tuberculifer*. All three pairs were able to discriminate between the *ferocior* and *swainsoni* tapes, and showed a response only to that of *ferocior*. The following field notes were made on November 6, 1974, along the Río Pilcomayo in Tarija, Bolivia:

Experiment 8—study area one, 5 km. from Villa Montes. Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. Experimental area is only a few meters from where I recorded dawn song from this male earlier this morning. One bird heard whistling up the slope at start at 6:33 A.M. One calling 40 ft. from *swainsoni* model in 30 seconds. Pair of *ferocior* about 50 ft. from *swainsoni* model in 1 minute; calling well over model at 6:35. A *tyrannulus* showed near *tyrannulus* model; making many passes over model. The *ferocior* moved out of experimental area at 6:37, but the pair of *tyrannulus* remained active near the *tyrannulus* model. Many passes by *tyrannulus*, and crisscrosses over *tyrannulus* area, calling well. No *ferocior* within experimental area at cable switch at 6:40. The *tyrannulus* reoriented within 20 seconds. More passes and crisscrosses in new *tyrannulus* area. A pair of *ferocior* appeared at the midpoint, briefly, then into 30 ft. of the new *swainsoni* model, calling sporadically. Calling high above *swainsoni* area. The pair of *tyrannulus* remained very excited in the new *tyrannulus* area, calling well. The pair of *ferocior* had left the experimental area by the end of the experiment, and could be heard calling outside the area. This could be a low level response of *ferocior* to *swainsoni* tape, or could be normal movement and activity of the pair, incidental to the playback.

Experiment 9—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. Tucumán *atriceps*. Start at 6:55 A.M. The *ferocior* began calling well up the slope in 20 seconds. Both birds over the *ferocior* model within 1 minute, calling excitedly. Crisscross at 6:57. One in to 6 ft. of *ferocior* model. Both within 30 ft. of *ferocior* model at 7:00. A *ferocior* calling well in new *ferocior* area within 1

minute following cable switch. At 10 ft. from new *ferocior* model at 7:03. Crisscross, calling well. Pass at the model at 7:04. Calling well within 15 ft. at 7:06. Calling well within 10 ft. of *ferocior* model at end of experiment. Good, strong response to *ferocior* playback.

The lower carrier frequency, the absence of hiccup notes in the daytime repertoire, and certain modifications of the roll (p. 510) readily differentiate the vocalizations of *ferocior* from those of *swainsoni*. With playback experiments I have been able to demonstrate that *ferocior* in Argentina and Bolivia and nominate *swainsoni* in Brazil do not respond to the playback of one another's vocalizations. Under simulated conditions of "sympatry" created by experimental playback, the two forms show the same indifference to each other's vocal repertoire that they show to the vocalizations of other species of *Myiarchus*. These findings suggest that if these forms were to come into contact and maintain the differences in vocal repertoires, they would behave toward one another as distinct species. Clearly, the next step was to document the vocal characters of the breeding birds in an area of potential and suspected contact of these forms and to conduct playback experiments in such an area.

The extensive collections made by William H. Partridge indicated that northeastern Argentina was one such area of contact between *ferocior* and *swainsoni*, and in November and December of 1970 I worked intensively with nine breeding pairs in Corrientes and Entre Ríos, Argentina (see fig. 39); the birds were intermediate morphologically (table 30). That these birds might behave differently from those in Tucumán and in São Paulo first became apparent during my reconnaissance for territorial pairs, for the birds appeared to respond readily to playback of either *ferocior* or *swainsoni*. After recording the vocal response of a few pairs that had been stimulated by playback, I realized that some birds were giving hiccup notes and some were not and I could hear both types of rolls (p. 510) characteristic of *ferocior* in Tucumán, as well as the typical roll of other subspecies of *M. swainsoni*. Furthermore, by collecting birds immediately after recording, I was able to establish that some individuals used

TABLE 30
**Reflectance Characteristics of the Back in
 Samples of *swainsoni* and *ferocior* and of
 Intergrades from the Zone of Contact^a**

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>swainsoni</i>	13	8.08	0.65	Standard	
Intergrades	15	8.64	0.82	2.6	3.4
<i>ferocior</i>	18	9.48	0.76	6.4	7.4

^aFrom the Argentine provinces of Corrientes and Entre Ríos (squares in fig. 39) and from central Paraguay (westernmost circle in fig. 39).

rolls of both *ferocior* and *swainsoni* in their repertoires. For example, among the rolls depicted in figure 33, graphs 8 and 9 were recorded from the same male (AMNH 822061) in Corrientes. In recordings of the vocal response of a pair in Entre Ríos, the male rendered rolls only of the *ferocior* type and gave no hiccup notes, but good hiccup notes were recorded from the female.

Eighteen playback experiments were conducted with five territorial pairs in Corrientes and Entre Ríos, using tapes of Tucumán *ferocior*, São Paulo *swainsoni*, *M. ferox*, and *M. tyrannulus*. In no instance did a pair consistently respond more strongly to one or the other of the *ferocior* and *swainsoni* tapes, and all were able to discriminate between these two tapes and those of other species of *Myiarchus*. The following field notes, made on November 16, 1970, in Corrientes, Argentina, illustrate the inability of these morphologically intermediate birds to discriminate between *ferocior* and *swainsoni* tapes, and show the strong response elicited by both tapes:

Experiment 5—study area one, Las Tres Marías, near Sombrero. Tapes used, Tucumán *ferocior* vs. *M. ferox*. One bird was whistling softly outside of experimental area about 5 minutes before start of experiment at 7:01 A.M. A bird appeared in the area within 30 seconds, giving rolls and rasping notes. Within 4 ft. of *ferocior* model at 7:02. In a study at 3 ft., calling excitedly. Pass at model at 7:03. Study at 1 ft. of *ferocior* model. Hovered just above model

at 7:04. Remained at 18 inches from model until 7:06, then attacked model, making contact only briefly. Returned to perch at 18 inches, giving rolls and rasping notes. Pass at model at 7:07; perching 12 inches on other side. Within 2 ft. of *ferocior* model at cable switch at 7:08. Reoriented to new *ferocior* area within 1 minute; perched 3 ft. from new model. Pass at new model at 7:10. Giving hiccup notes and rasping notes, and rolls. Strong vocal response, 2 ft. from *ferocior* model. Another pass at 7:14. Another attack on *ferocior* model at 7:15. Still calling within 2 ft. of model at end of experiment. (At 7:17 it again attacked the *ferocior* model, though the speaker was silent.)

Experiment 6—same locality, pair, and date as above. Tapes used, *M. tyrannulus* vs. *M. ferox*. Start at 7:19 A.M., with birds silent and out of experimental area. At 7:22, a pair of *M. tyrannulus* showed in the *tyrannulus* area (had not realized they were also territorial here). They moved out to midpoint at 7:23, then a single *M. swainsoni* chased the pair of *M. tyrannulus* briefly. The pair of *M. tyrannulus* moved back to 4 ft. of *tyrannulus* model, and *M. swainsoni* disappeared. *M. tyrannulus* in a pass at *tyrannulus* model at 7:24. Calling well 5 ft. from *tyrannulus* model. Both *tyrannulus* within 20 ft. of model at 7:25. Cable switch at 7:26; the *tyrannulus* reoriented within 20 seconds, to within 6 ft. of new *tyrannulus* model. To 18 inches of new model, calling excitedly. Discontinued this experiment at 7:30, in order to try next crucial experiment. The *M. swainsoni* did not reappear in this experiment.

Experiment 7—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. São Paulo *swainsoni*. All birds had become silent by the start of this experiment at 7:34 A.M. One *M. swainsoni* appeared in 1 minute, calling about 30 ft. from *swainsoni* model. Reoriented to *ferocior* area, 5 ft. from model, at 7:35:30. Calling well. Attacked the *ferocior* model twice at 7:36. Back to midpoint, giving rasping notes, then back to *ferocior* model at 7:37. Over to *swainsoni* area at 7:38. To 7 ft. of *swainsoni* model at 7:39. Back over to *ferocior* area at 7:40, still calling excitedly. Back to midpoint, then over to *ferocior* area, giving rasps and rolls. To 2 ft. of *ferocior* model at 7:41. Back to *swainsoni* area just before cable switch at 7:42. Pass at new *ferocior* model within 20 seconds. Attack on new *ferocior* model at 7:43. Back to midpoint, then return to 20 ft. of *ferocior*. Over to *swainsoni* at 7:44; to within 3 ft. of *swainsoni* model, giving rasps and rolls, and hiccups. Attack on *swainsoni* model at 7:45. Back to *ferocior* area, 6 ft. from model. To within 2 ft. of *ferocior* model at 7:46. Crisscross of

ferocior area. Attack on *ferocior* model at 7:47. Out to midpoint, then back to *ferocior* at end of experiment. Only a single bird has responded in this series. Gave it a 10-minute rest before beginning the following experiment.

Experiment 8—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. All birds silent at start at 8:00 A.M. A *M. tyrannulus* began calling within 20 seconds. The *tyrannulus* appeared in *tyrannulus* area in 1 minute. In a pass at *tyrannulus* model at 8:02. A single *M. swainsoni* showed at 25 ft. of *swainsoni* model, then in to 6 ft. of model. Pass by *M. swainsoni* at *swainsoni* model, giving hiccup notes. The *tyrannulus* is in a study at 8 ft. from *tyrannulus* model. The *M. swainsoni* attacked the *swainsoni* model at 8:04. The *tyrannulus* attacked the *tyrannulus* model. A pass by *M. swainsoni* on the *swainsoni* model at 8:05. Study by *M. swainsoni* at 2 ft. from *swainsoni* model. Cable switch at 8:07. The *tyrannulus* reoriented, and then the *M. swainsoni* reoriented to 2 ft. of new *swainsoni* model. A crisscross by *tyrannulus* in the new *tyrannulus* area. A pass by *M. swainsoni* at new *swainsoni* model. The *tyrannulus* moved in to 3 ft. of new *tyrannulus* model. Another pass by *M. swainsoni* on *swainsoni* model at 8:10. Another pass by *M. swainsoni*, and a crisscross by *tyrannulus* at 8:10:30. A pass by *tyrannulus* at the *tyrannulus* model, then another pass. A brief attack on *swainsoni* model by the single *M. swainsoni*. Crisscross by *M. swainsoni*, giving rasps and hiccup notes. End experiment with *M. swainsoni* 6 ft. from *swainsoni* model, still calling well.

Data from my playback experiments and from recordings of birds subsequently collected are insufficient to indicate precisely the width of this zone of contact in which territorial *M. swainsoni* will respond to playback of either Tucumán *ferocior* or São Paulo *swainsoni*.

My only field experience immediately to the east was in Maldonado, Uruguay, about 300 km. east of the zone of morphological intermediacy (see fig. 36). No playback experiments were conducted, but the three pairs recorded and collected there were not separable vocally or morphologically from nominate *swainsoni* in São Paulo. Near El Tío, in Córdoba, Argentina, about 300 km. west of the zone of morphological intermediacy, I was able to conduct a series of playback experiments. The following field notes were taken on December 3, 1970:

Experiment 44—study area of territorial pair with vocal characters typical of Tucumán *ferocior*. Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. No birds heard calling prior to start, and their location unknown. Site selected on the basis of recordings made here yesterday. Start at 6:31 P.M. Heard a *ferocior* type roll outside experimental area at 6:31:30. One bird appeared 40 ft. from *swainsoni* model at 6:32, and gave several rolls. It flew 50 ft. outside experimental area at 6:33. Flew to 30 ft. beyond *tyrannulus* model, gave another roll. Not particularly excited or vocally responsive. Another roll at 6:34. It moved to midpoint at 6:34:30, gave another roll. Flew about 30 ft. beyond *swainsoni* model, silent. Then gave another roll at 6:35. Flew 50 ft. outside experimental area at 6:35:30. Moved farther out of area at 6:36. Giving a few rolls outside area at cable switch at 6:38. The bird remained out of experimental area after the cable switch. Not a single roll heard during entire second half of the experiment; whereabouts of this bird unknown in second half.

Experiment 45—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. Tucumán *atriceps*. No birds calling prior to start, location unknown. Start at 6:49 P.M. One bird appeared at 6:52, giving good rolls. To midpoint at 6:53, still giving rolls. Over to 30 ft. from *atriceps* model at 6:54, giving good rolls. To 15 ft. of *atriceps* model. Back to midpoint at 6:54:30. Over to 8 ft. from *ferocior* model by 6:55. Giving rolls. Still 10 ft. from *ferocior* model at cable switch, at 6:56. To midpoint within 1 minute, calling excitedly. Didn't reorient to new *ferocior* model until 6:58, but then moved to 30 ft. of the new model, calling well. Attacked the new *ferocior* model at 7:00. Giving excited rolls at 8 ft. behind model. Out to midpoint at 7:01. Disappeared from my view briefly, then reappeared with a second bird. Both birds remained within *ferocior* area for remainder of the experiment.

Experiment 46—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. São Paulo *swainsoni*. Occasional roll heard from outside experimental area just prior to start at 7:08 P.M. One bird appeared within 1 minute, giving rapid rolls, 40 ft. from *ferocior* model. To 10 ft. of *ferocior* model by 7:11, giving rolls all the time. Still 10 ft. from model at 7:13, giving rolls. In a study at 8 ft. at 7:14. Still in that study at cable switch at 7:15. Moved over to midpoint by 7:16, giving rolls. To 40 ft. of new *ferocior* model by 7:16:30. In to 20 ft. of new *ferocior* model at 7:17, still giving rolls. In study at 12 ft. of *ferocior* model, giving rolls, at 7:19. Out to midpoint briefly at 7:21, but back to 30 ft. of *fero-*

cior model in 30 seconds. In to 10 ft. of model at end of experiment, giving good rolls. Good demonstration of ability to discriminate between Tucumán *ferocior* and São Paulo *swainsoni* tapes.

I had another opportunity to test *ferocior* less than 100 km. west of the zone of morphological intermediacy, along the Río Paraná about 30 km. NE of Santa Fe, Santa Fe, Argentina. My recordings of this pair of territorial birds demonstrate that their vocal characters were typical of *ferocior*. The male was collected subsequently (AMNH 822043), had gonads in breeding condition, and was morphologically typical of *ferocior*. The following field notes were taken on December 4, 1970:

Experiment 50—Tapes used, São Paulo *swainsoni* vs. *M. tyrannulus*. Pair originally found with *swainsoni* reconnaissance tape. Giving sporadic rolls outside experimental area a few minutes prior to start at 6:43 P.M. No show at all, in either half of experiment, even though I oriented speaker toward four compass directions.

Experiment 51—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. Tucumán *atriceps*. No birds have been heard since several minutes prior to start of experiment 50. Start at 7:01 P.M. A bird appeared in *ferocior* area within 30 seconds. In a study at 20 ft.; gave a rasping note, and a roll. Attacked the *ferocior* model, then into a study at 6 ft., giving rasps. Another attack at 7:05, then hovered over the *ferocior* model. Has given only rasps and rolls, no hiccups. A pass, then out to 20 ft. of *ferocior* model. Another pass at 7:06, and more rasps. Another pass. Another pass. Crisscross to 30 ft. on other side of *ferocior* model. More rolls, after a pass to within 20 ft. of model. Pass at 7:07. In a study at 15 ft., giving rasps and rolls. Pass, out to 20 ft. Two more passes. An attack on *ferocior* model just prior to cable switch at 7:08. Bird in a study, 6 ft. from *ferocior* model at the switch. Reoriented to within 20 ft. of new *ferocior* model within 30 seconds. Pass at new model at 7:09:30. In a study at 8 ft. from model. Out to 40 ft., giving rolls and rasps. Pass at 7:11, then in to 10 ft. of *ferocior* model. Another pass; two more passes. In to 6 ft. of model. An attack at 7:13. Almost continuous rolls and rasps—very excited. Pass at 7:14. Out to 10 ft. of model. Calling within 8 ft. of *ferocior* model at end of experiment.

Experiment 52—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. Tucumán *ferocior*, to test stimulus value of *swain-*

soni tape now that this bird has been stimulated by previous experiment. Start at 7:21 P.M. Bird giving occasional roll just out of experimental area at start. Oriented at once to the *ferocior* model. Pass at model, then in to 10 ft., giving rasps and rolls. In a study at 10 ft., then another pass. Study at 8 ft., more rasps and rolls. An attack on *ferocior* model at 7:24. Study at 4 ft. Pass at 7:25. Another attack, then in a study at 3 ft. Another pass, and out to 6 ft. Another attack on *ferocior* model at 7:27. Almost continuous rolls and rasps (no hiccups!). Another attack. In a study at 4 ft. Pass at 7:25:30. Cable switch at 7:28, when bird was 6 ft. from model. Reoriented within 30 seconds (i.e., left *swainsoni* speaker, and crisscrossed new *ferocior* model at 7:29). In a study at 6 ft., still calling well. Study at 3 ft. from *ferocior* model. Another pass. Another pass. An attack on *ferocior* model at 7:31. Pass at 7:32. In a study at 10 ft., calling well. Another attack at 7:23. Pass. Another attack, and in a study at 6 ft. Attack on *ferocior* model again at 7:34. At 7:35 flew over to *swainsoni* area, but within 30 seconds had returned to *ferocior* area where it attacked the *ferocior* model just as the experiment ended. No question about this bird's ability to discriminate between *ferocior* and *swainsoni* tapes. No evidence that the *swainsoni* tape has anything but minimal stimulus value.

These data suggest that an inability to discriminate between the playback tapes of Tucumán *ferocior* and São Paulo *swainsoni* may be limited to populations less than 100 km. on either side of the zone in which intermediacy in morphology and vocal characters can be demonstrated.

MORPHOLOGICAL INTERGRADATION BETWEEN *swainsoni* AND *ferocior*

Zimmer (1938a) wrote: "Intergradation between *swainsoni* and the still larger *ferocior* may be presumed to occur in Uruguay where *ferocior* is reported to exist in the western part of the country and *swainsoni* in the east." Zimmer was handicapped by a lack of adequate material to verify intergradation between these forms, but fortunately recent fieldwork in Argentina and Paraguay has provided such proof. As a result of extensive collections made by William H. Partridge (American Museum of Natural History and Museo Nacional de Historia Natural) in northeastern Argentina, and

Jacob Unger (American Museum of Natural History and Field Museum) in central Paraguay, and of my field work in northeastern Argentina, it is now possible to delimit a comparatively narrow zone of intergradation between these forms (fig. 39). The zone runs almost due north and south, from central Paraguay south through the Argentine provinces of Corrientes and Entre Ríos to extreme southwestern Uruguay. The specimens from this zone are intermediate in all characteristics, including both mensural characters (tables 22, 23) and plumage coloration (table 30 and fig. 40).

Steinbacher's reports (1962, 1968) on a series of six specimens taken by Jacob Unger in the chaco of central Paraguay deserve special comment here. Even though Steinbacher ac-

knowledgeed that this series appeared to be longer-winged and shorter-tailed than suggested in published data for *M. ferox australis*, he preferred to assign all of them to that form. While I have not examined the specimens, the measurements given certainly suggest *M. swainsoni* rather than *M. ferox*. I have seen 15 other specimens taken by Unger in the chaco of west-central Paraguay; thirteen of these I regard as being intergrades between *swainsoni* and *ferocior*, and the other two are migrant *swainsoni*. I have seen no specimens of *M. ferox australis* from west of the Río Paraguay in Paraguay, and my experience with this form leads me to doubt its presence in chaco habitat at any appreciable distance from the pantanal (wet palm savanna) along the Río Paraguay.

Specimens of intergrades between *ferocior*

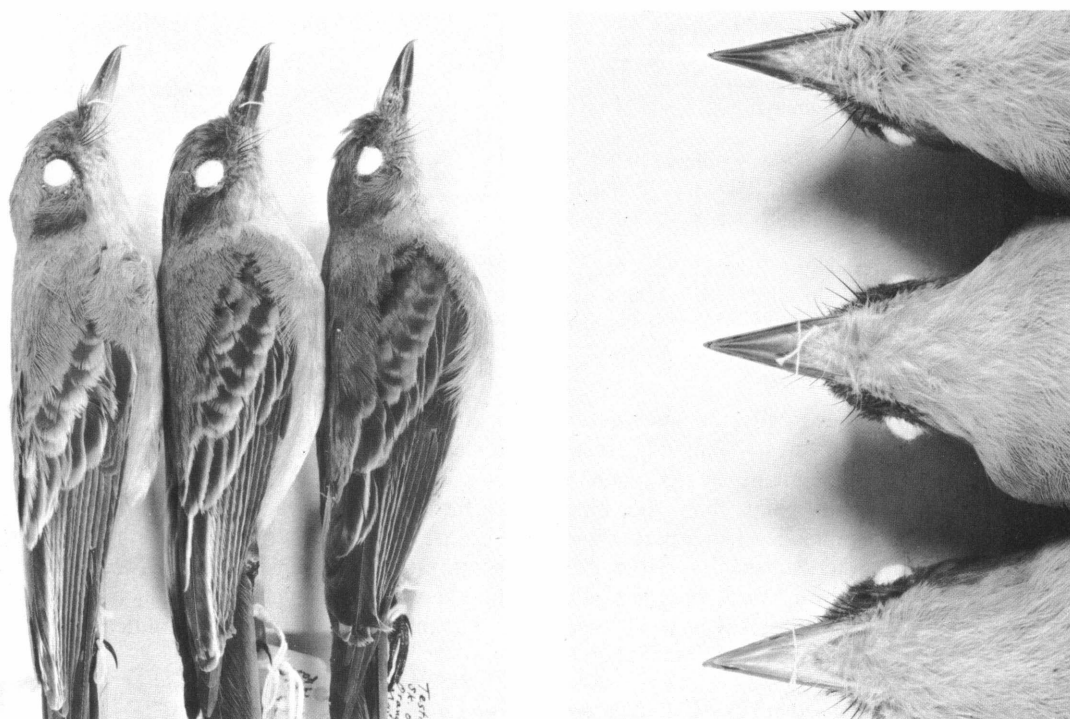


FIG. 40. Intergradation between *Myiarchus swainsoni swainsoni* and *M. s. ferocior*. Left: General plumage coloration, extent of white in wing, and prominence of dark auriculars; (left to right) *ferocior* from Tucumán (AMNH 822054), intergrade from Corrientes (AMNH 822061), and *swainsoni* from São Paulo (AMNH 822093). Right: Bill color; (top to bottom) *swainsoni* from São Paulo (AMNH 822093), intergrade from Corrientes (AMNH 822061), and *ferocior* from Tucumán (AMNH 822055). All collected during breeding season, within a three year period, and hence in comparable plumage.

and *swainsoni* examined, 82; localities, by country, from north to south and west to east (see fig. 39; asterisks denote author's study areas): PARAGUAY, Orloff, Chaco (Lichtenau); Puerto Casado, Chaco; Nueva Italia, Paraguari. ARGENTINA, *Las Tres Marias, Corrientes (Corrientes; San Luis del Palmar); Itatí, Corrientes; Concepción, Corrientes; Carlos Pellegrini, Corrientes; Mercedes, Corrientes; *Concordia, Entre Ríos; Concepción del Uruguay, Entre Ríos. BRAZIL, Barra do Quaraí, Rio Grande do Sul. URUGUAY, San Gregorio, Artigas; Nueva Palmira, Colonia (Dolores, Soriano).

Wintering specimens examined, 1; locality: VENEZUELA, Caicara, Bolívar (see fig. 38).

Myiarchus swainsoni phaeonotus
Salvin and Godman

Myiarchus phaeonotus Salvin and Godman, 1883, p. 207 (type locality, Merumé Mts., British Guiana; cotypes in the British Museum [Nat. Hist.]). Todd, 1922, p. 197. Hellmayr, 1927, p. 174 (synonymy).

Myiarchus swainsoni phaeonotus: Zimmer, 1938a, p. 9 (new combination). Pinto, 1944, p. 172. Phelps and Phelps, 1963, p. 188. Meyer de Schauensee, 1966, p. 351.

Myiarchus swainsoni fumosus Zimmer and Phelps, 1946, p. 10 (type locality, Mt. Ptari-tepui, Bolívar, Venezuela; holotype in the Phelps Collection, on deposit in the American Museum of Natural History, examined).

DIAGNOSIS: Morphologically the most divergent of all the subspecies. Mandible black throughout in fresh specimens. Outer vane of outer rectrix dark, not paler than the inner vane, even in fresh plumage. Upperparts much darker than in all other subspecies (table 28). Gray of throat as in *swainsoni*, but abdomen paler (less yellow, more white) than in all other subspecies. Wing slightly less pointed than in the other subspecies.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 41): Restricted to tropical and subtropical zones of southeastern Venezuela, western Guyana, and the upper Rio Negro and Rio Branco, Brazil. Intergrades with *pelzelni* over a rather extensive area, including eastern Guyana, Surinam, along the Amazon from Santarem westward to Manaus, and along the

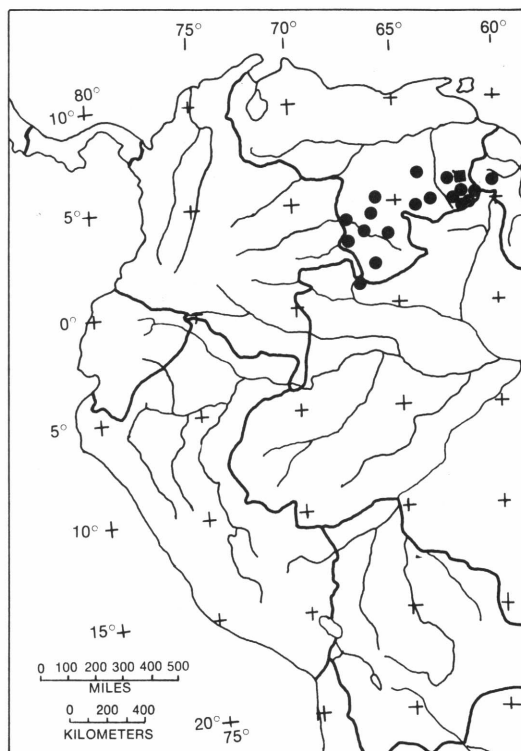


FIG. 41. Distribution of *Myiarchus swainsoni phaeonotus* as indicated by localities of specimens examined (circles) and by site where author studied this taxon in the field (square). See page 530 for a list of these localities and page 512 for an itinerary of author's fieldwork with this taxon.

lower Rio Negro and Rio Branco, Brazil (fig. 37). Nonmigratory.

Initially considered a strictly montane form, because the known range was confined to the subtropical elevations of southeastern Venezuela and western Guyana. Subsequent collections from the upper Rio Negro indicate a much broader range of habitats.

Sympatric with *M. ferox* and *M. tuberculifer* throughout its range, but only locally with *M. tyrannulus*, in drier habitats.

Specimens examined, 80; localities, by country, from north to south and west to east (see fig. 41; asterisk denotes author's study area): VENEZUELA, Cerro Tonoro, Bolívar; Cerro Auyan-tepui, Bolívar (Cerro Uaipán-tepui); *Kavanayén, Bolívar (Cerro Ptari-tepui);

Cerro Acopán-tepui, Bolívar; Cerro Roraima, Bolívar (Arabupú; Cerro Uei-tepui); San Juan de Manapiare, Amazonas; Río Carún, Bolívar; Cerro Itebe-tepui, Bolívar; Hata Santa Teresa, Bolívar; Cerro Sarisariñama, Bolívar; Río Ica-barú, Bolívar; Río Asisa, Amazonas; San Fernando de Atabapo, Amazonas; Puerto Yapacana, Amazonas (Cerro Yapacana); Cerro Duida, Amazonas (Cerro Marahuaca); Pimichín, Amazonas (Río Temí); Río Yatúa, Amazonas. GUYANA, Merume Mts. BRAZIL, Cucuhy, Amazonas.

RELATIONSHIP OF
phaeonotus WITH *Myiarchus swainsoni*

Most early workers, with inadequate material, maintained *phaeonotus* as a distinct species, while recognizing its close affinity with *swainsoni* and *pelzelni* on the basis of the relatively short tail and shape of the wing (Todd, 1922; Hellmayr, 1927). Hellmayr admitted that it "is perhaps merely a local race of *M. swainsoni*, but the only available specimen not being in very good condition does not admit of final conclusion." Extensive collecting by the Phelps in Venezuela and recent fieldwork in Surinam have added to our knowledge of the distribution of this form and have provided a better framework for determining its relationship with *M. swainsoni*.

Zimmer described *M. swainsoni amazonus* (1938a) from the lower Amazon as a form connecting *phaeonotus* to *pelzelni*, geographically and morphologically, and concluded that "there seems to be no good reason to keep *phaeonotus* specifically distinct from *swainsoni* and *pelzelni*." He believed that he had sufficient material to demonstrate a gradation in wing shape and in plumage coloration from *pelzelni* through *amazonus* to *phaeonotus*, and many but not all subsequent authors have followed him. Todd wrote to Zimmer on April 3, 1951: "I cannot help but feel that your *amazonus* is also too close to *pelzelni* for formal separation," and Mees (1968) also chose not to recognize *amazonus*, thereby keeping *pelzelni* and *phaeonotus* specifically distinct.

These two forms, *phaeonotus* and *pelzelni*, are about as distinct morphologically as any two *species* in the genus. I have reexamined

the specimens that were available to Zimmer, and have looked at additional material collected subsequently, including critical specimens taken by Haverschmidt, Mees, and myself in Surinam. I agree with Zimmer that *phaeonotus* intergrades with *pelzelni* throughout an extensive area that extends from Guyana and Surinam south through equatorial Pará and Amazonas, Brazil (fig. 37). The intergradation with respect to wing shape is demonstrated in tables 25 and 26, and table 31 and figure 42 show the intergradation in the coloration of the upperparts and the bill. Specimens from this extensive contact zone also suggest that these morphologically intermediate populations also possess a breeding and molt cycle that is intermediate between those of *phaeonotus* and *pelzelni*. Typical *pelzelni* breeds from September through December, and undergoes the prebasic molt from December to May. Typical *phaeonotus* breeds from February to May, and molts from March to August. The only reference that I find for breeding in this intermediate zone is that of Mees (1968), who collected a recent fledgling in southern Surinam in June. A specimen (ANSP 51372) taken in Guyana on April 22 is in juvenal plumage. A large series of Surinam specimens suggests that the season for the prebasic molt in that region extends from July through December, almost exactly intermediate between the seasons of molt in *pelzelni* and *phaeonotus*.

Special comment should be made here on the specimens of *M. swainsoni* that have been taken in Surinam, since that region is signifi-

TABLE 31
Reflectance Characteristics of the Back in
Samples of *phaeonotus* and *pelzelni* and of
Intergrades from the Zone of Contact^a

Sample	N	Brightness (Percent)		Color Difference (MacAdam Units)	
		Mean	S.D.	DL	DE
<i>phaeonotus</i>	11	5.22	0.44	Standard	
Intergrades	11	7.11	0.64	11.3	11.7
<i>pelzelni</i>	9	9.83	0.74	27.5	28.1

^aSample includes specimens from Guyana, Surinam, and Pará and Amazonas, Brazil (fig. 37).

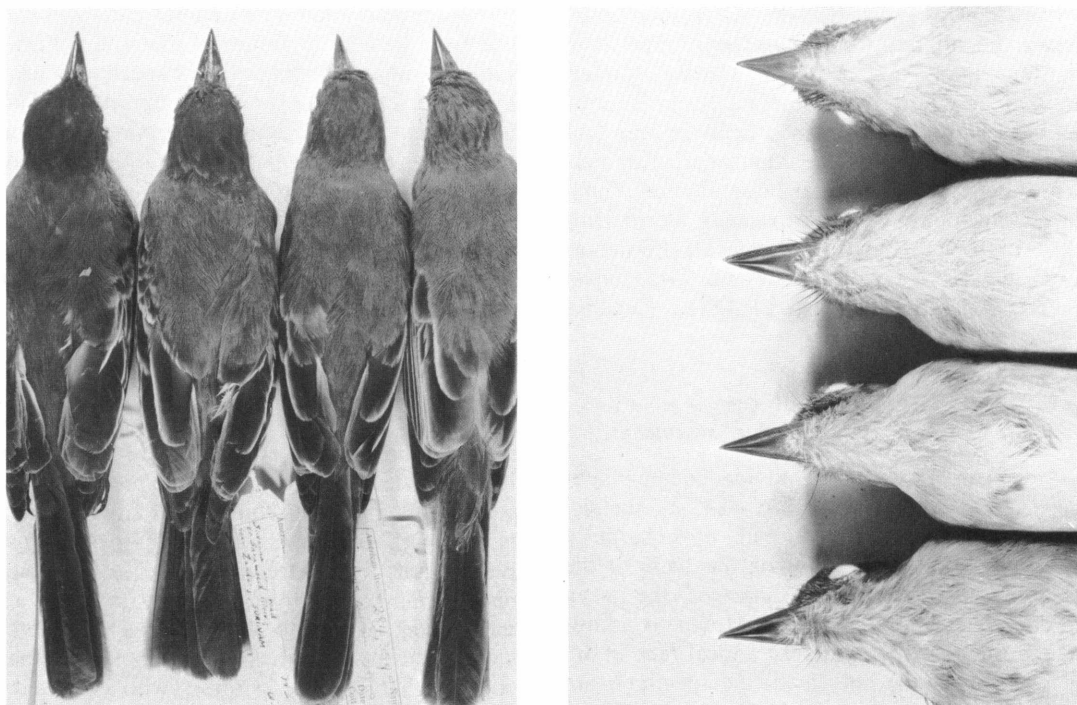


FIG. 42. Intergradation between *Myiarchus swainsoni phaeonotus* and *M. s. pelzelni*. Left: General coloration of upperparts; (left to right) *phaeonotus* from Venezuela (PC 27362, type of “*fumosus*,” August 1944), intergrade from Surinam (AMNH 822012, December 1970), intergrade from Pará (AMNH 284359, type of “*amazonus*,” November 1930), and *pelzelni* from Peru (AMNH 145398, July 1916). Right: Bill color; (top to bottom) *pelzelni* from Bahia (AMNH 822016, December 1967), intergrade from Surinam (AMNH 822013, December 1970), intergrade from Surinam (AMNH 822011, December 1970), and *phaeonotus* from Venezuela (AMNH 822008, May 1969).

cant in any discussion of the relationship between *phaeonotus* and the other forms of *M. swainsoni*. Haverschmidt (1968) took five specimens in northern Surinam, assigning them to the nominate race and considering them migrants; until then, the species had not been recorded in Surinam. The presence of wintering nominate *swainsoni* in Surinam was plausible, since that migratory form winters regularly in Venezuela, Trinidad, and Guyana. Then Mees (1968) took an important series of specimens, including a fledgling still being fed by its parents, from Sipaliwini in southern Surinam. Mees assigned his specimens to *M. p. pelzelni*, thereby expressing disagreement with Zimmer’s conclusion that *pelzelni* and *swainsoni* are conspecific. I have examined both of these series from Surinam and conclude that both represent

a resident Surinam population that is morphologically intermediate between *phaeonotus* and *pelzelni*.

My first clue that something might be amiss with Haverschmidt’s (1968) identification of his series as wintering nominate *swainsoni* was the fact that one of these birds had been collected on January 5, at a time when nominate *swainsoni* is breeding in southern Brazil and Uruguay. Upon examining the series I found another specimen, taken in mid-September, in the middle of a molt of the remiges. Wintering *swainsoni* complete their wing molt on the wintering grounds—but by August. Mees’s series established without doubt the presence of a resident member of this complex in southern Surinam. My reidentification of Haverschmidt’s series of specimens from northern Surinam sug-

gested that the resident form also extends northward to the coast.

The possibility that there was a resident population of *M. swainsoni* in Surinam needed confirmation by actual field work in that country. In response to a letter in which I outlined my hypothesis and supporting arguments, Haverschmidt wrote that he was doubtful that *M. swainsoni* bred in northern Surinam but that he would be willing to take me to some of the localities where he had collected his birds. On December 20, 1970, Haverschmidt and I visited the Hannover savanna, near Zanderij, where I was able to locate a pair of resident *M. swainsoni*, using a reconnaissance tape made from a recording of nominate *swainsoni* in São Paulo, Brazil. The next day, following a series of playback experiments (discussed on p. 520), both birds were collected and found to be in nonbreeding condition and completing their prebasic body molt. Based on the condition of the plumage, I judged that they had bred sometime during the period of June through August. Morphologically, these and three other specimens that I took near Zanderij were intermediate between *phaeonorotus* and *pelzelni* (see table 31 and fig. 42).

INTERPRETATION AND SIGNIFICANCE OF PLAYBACK EXPERIMENTS

I was not surprised that I was able to locate a resident Surinam population using a reconnaissance tape made from nominate *swainsoni* repertoire because I had already determined, from my fieldwork with *phaeonorotus* in Venezuela, that there were no differences between the vocal characters of *phaeonorotus* and *swainsoni* (p. 510). I had had no difficulty locating pairs of *phaeonorotus* in Venezuela using the same reconnaissance tape. Playback experiments with *phaeonorotus* further document the responsiveness of that form to *swainsoni* repertoire and support the view that they are conspecific. They also demonstrate an ability of *phaeonorotus* to discriminate between tapes of *ferocior* and *swainsoni*, as does *swainsoni* in São Paulo, Brazil. The following notes were made in a *phaeonorotus* territory at Kavanayén, Bolívar, Venezuela, on May 1, 1969:

Experiment 1—study area one. Tapes used, Tucumán

ferocior vs. São Paulo *swainsoni*. Birds silent, location unknown. Start at 9:00 A.M. No show at all; oriented speaker in various directions, but no luck. Birds apparently out of range. One bird heard just outside experimental area at end of this experiment.

Experiment 2—same locality, pair, and date as above. Tapes used, as above. Start at 9:15. A bird became vocal to one side of *ferocior* area. Crossed over to *swainsoni* area at 9:17, to within 30 ft. of the model, calling well. Two birds calling well in *swainsoni* area at 9:19, within 30 ft. of model. One crossed over to *ferocior* area at 9:20, but returned to *swainsoni* area within 10 seconds. Crisscross of *swainsoni* model at 9:21:30. To within 30 ft. of *swainsoni* model at cable switch. Both birds re-oriented to new *swainsoni* area within 30 seconds. One calling well 50 ft. from new *swainsoni* model at 9:25. At 9:25:30 crossed over to *ferocior* area; perched 20 ft. from *ferocior* model for 30 seconds, then returned to *swainsoni* area. Both birds within 30 ft. of *swainsoni* model. Both crisscrossed mount. Both still within 30 ft. of *swainsoni* model, calling well, at end of experiment.

Experiment 3—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. *M. oberi*. To test stimulus value of *ferocior*, without the simultaneous stimulation of *swainsoni* tape. Birds still calling well out of experimental area at start at 9:35. One bird showed in *ferocior* area, 40 ft. from model, at 9:37. Both birds about 50 ft. from *ferocior* model at 9:39 (they were on that side of experimental area at start of experiment). Both calling 40 ft. from *ferocior* model at 9:41. One moved to within 20 ft. of model at time of cable switch at 9:42. Birds remained within 25 ft. of new *oberi* model, then, at 9:45, moved out to 70 ft. from *oberi* model and outside of experimental area. At 9:45:30, one moved to within 60 ft. of new *ferocior* model, fairly vocal. Became silent by 9:47. Bird is preening, only occasionally vocalizing; other bird's location unknown at end of experiment. Interpreted as a very low level response to *ferocior*, and possibly a residual effect from stimulation received in experiment 2.

Experiment 4—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. São Paulo *swainsoni* once again. Birds silent at start at 9:53. One bird flew into *swainsoni* area within 15 seconds. Both birds there, calling excitedly, at 9:54, within 45 ft. of model. Both birds crossed over to *ferocior* area at 9:55. One back to *swainsoni* area within 30 seconds, and both there by 9:57. Calling well within 40 ft. of *swainsoni* model at cable switch at 10:00.

Birds reoriented at once, calling well within 40 ft. of new *swainsoni* model. One bird flew back to *ferocior* area briefly, then returned to *swainsoni* area, calling well within 30 ft. of model. Crisscrossed *swainsoni* model at 10:04. Another crisscross. Both birds in *swainsoni* area at end of experiment. Good response to *swainsoni*, with possible low level response to *ferocior*.

Experiment 5—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. *M. venezuelensis*, to test birds after a 20 minute rest period. Birds had been silent, location unknown, for over 15 minutes prior to start at 10:27. No show in first seven minutes of playback, so discontinued this experiment and proceeded with the next one.

Experiment 6—same locality, pair, and date as above. Tapes used, Tucumán *ferocior* vs. São Paulo *swainsoni*. Birds haven't been heard for nearly 25 minutes; start at 10:36. One bird showed within 15 seconds, quite vocal, at midpoint. Moved to within 25 ft. of *swainsoni* model, calling well, at 10:37. To within 20 ft. at 10:40. Both birds about 30 ft. from *swainsoni* model by 10:42. Crisscross at 10:43. Still there at cable switch at 10:44. One bird still calling from new *ferocior* area at 10:46, but had reoriented to new *swainsoni* model by 10:47. Crisscross over new *swainsoni* model at 10:48:30. Calling 30 ft. from *swainsoni* model, but out to midpoint at end of experiment. Confirmation of good response to *swainsoni* tape and ability to discriminate between *ferocior* and *swainsoni* tapes!

A second pair of *phaeonotus* at Kavanayén, tested on May 3, 1969, also demonstrated a similar responsiveness to *swainsoni* tape:

Experiment 7—study area two. Tapes used, Tucumán *ferocior* vs. *M. nugator*. No prior stimulation with *swainsoni* tape. Birds heard in general area five minutes before experiment. Start at 8:25 A.M. No show and no vocalizations during first seven minutes. Cable switch at 8:32. At 8:34 one bird could be heard calling outside the experimental area. No show during rest of the experiment.

Experiment 8—same locality, pair, and date as above. Tapes used, São Paulo *swainsoni* vs. *M.*

nugator. Start at 8:43 A.M. One bird oriented to *swainsoni* area within 15 seconds, calling well. Both birds within 45 ft. of *swainsoni* model, calling. In to 30 ft. by 8:44. To 25 ft., calling excitedly, at 8:45. Out to midpoint at 8:45:30, but back to *swainsoni* area by 8:46. Both birds within *swainsoni* area at cable switch at 8:50. One moved out to midpoint within 15 seconds. Both birds within new *swainsoni* area by 8:51, calling well. One 25 ft. from *swainsoni* model at 8:52. Calling about 20 ft. from model at 8:53, and stayed there in a study until end of experiment. Good differential response!

DISCUSSION: The morphological, geographical, and behavioral evidence presented here confirms Zimmer's earlier conclusion that *phaeonotus* should be considered a subspecies of *M. swainsoni*, and that the intergradation between the two morphological extremes within the species, *phaeonotus* and *pelzelni*, occurs throughout an extensive area as illustrated in figure 37. I have chosen not to recognize Zimmer's "*amazonus*" for this intermediate population, but simply to designate such specimens as intergrades between *phaeonotus* and *pelzelni*. This particular contact zone between adjacent, well-marked subspecies differs only in its larger size from two others that I have discussed in detail and chosen not to designate by formal name: (1) that between *ferocior* and *swainsoni* (p. 528), and (2) that between *brunnescens* and *ferox* (p. 575).

Specimens of intergrades between *pelzelni* and *phaeonotus* examined, 50; localities, by country, from north to south and west to east (see fig. 37; asterisk denotes author's study area): GUYANA, Rockstone; Annai. SURINAM, *Zanderij (Paramaribo; Leonsberg); Sipaliwini. BRAZIL, Serra da Lua, Rio Branco (Bôa Vista); Pôrto Santana, Amapá; Tabocal, Amazonas (Yavanari); Faro, Pará; Santarém, Pará (Igarape Brabo); Tonantins, Amazonas; Manáos, Amazonas (Cacao Pereira); Itacoatiara, Amazonas; Tauary, Pará; Fordlandia, Pará; Santo Antonio de Guajará, Amazonas.

MYIARCHUS APICALIS SCLATER AND SALVIN

This monotypic and well-marked Colombian endemic has one of the most restricted geographical ranges of any species in the genus. The known range is limited to the upper por-

tions of four river systems in west central Colombia: Dagua, Cauca, Patía, and Magdalena (fig. 46). The species is nonmigratory.

DIAGNOSIS: Rectrices with conspicuous and

extensive whitish tips; pale tip of outer rectrix measures at least 8 mm. along rachis. Rectrices of adults not marked with Antique Brown. In fresh specimens, entire mandible black; no seasonal or geographical variation; but paling occurs, rendering the character unreliable in older museum specimens. Color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics consists of repeated rolls delivered in long bouts, but has *no* rasps. Dawn song unknown.

HABITAT (FIG. 43): Tropical zone primarily, though some individuals extend up into the lower subtropical at least in the Departments of Valle and Cauca. Arid and semiarid savannas, thinly forested regions, and riparian woodlands.

BREEDING AND ANNUAL CYCLE: *Myiarchus apicalis* presumably is a cavity nester, although I found no nest and know of no reference in the literature. The breeding behavior of this species is an enigma to me, for I failed to locate any males giving dawn song during intensive fieldwork from late January to late April in three different years. Miller (1947) wrote: "On January 19 a sexually inactive female was watched investigating a hole in a fence post at the edge of streamside woods. A male in breeding condition was taken near here on January 23." Males collected from late January to mid-April have been noted as having enlarged gonads. One that I collected on March 25 had testes measuring 10 by 6 mm., whereas one in heavy molt on April 16 had testes that measured only 3 by 2 mm. The species appears to breed from January through April in all parts of its range. I have seen two juvenals: one that I collected near Cali on April 16, and one taken by Carriker on July 10.

The definitive basic plumage is replaced during a complete annual molt that follows breeding. Specimens showing active molt of the remiges have been taken from March through August.

VOCAL CHARACTERS: The analysis of vocal characters of *M. apicalis* is based on recordings from these samples: Valle, Colombia, seven pairs; Cauca, Colombia, one pair; Huila, Colombia, three pairs.

CALLS: The vocal repertoire of this species, as determined from the recordings noted above,

is summarized in table 1 and illustrated in figures 44 and 45.

In response to playback, or when excited by intruding conspecifics, *M. apicalis* vocalizes with repeated rolls, hiccups, and series of whistled notes. The most conspicuous calls in this vocal response are the rolls, which can be quite variable in duration, apparently reflecting degrees of motivation and excitement (fig. 44). Normally, the component syllables of the roll are chevron-like ("huit") notes. Unlike *M. tuberculifer* and *M. swainsoni*, the only other South American species with similar rolls, *M. apicalis* typically gives long bouts of rolls without the intervention of other types of calls. Occasionally the roll will blend almost imperceptibly into a hiccup note, or into a series of whistles. The hiccup (fig. 45) is nearly identical with that of *M. tuberculifer* but at a lower frequency (due to larger body size). Whistled notes vary in duration and configuration (fig. 45:14-23), but tend to be plaintive and of low amplitude. Their close relationship to and association with the roll is apparent in figure 45. When the whistled notes are brief, the traces become chevron-like and can be classified as "huit" notes (fig. 45:13). This is another illustration of the continuum among the various basic types of calls, depending upon how the carrier frequency is modified. The complete absence of any type of rasping note is diagnostic of this species.

DAWN SONG: Despite repeated efforts over several years, I have been unable to record the dawn song of *M. apicalis*, the only species that I lack among the South American species. On the basis of its relationship with other "whistlers" (see table 1), including *M. swainsoni* and *M. phaeocephalus*, one might predict that *M. apicalis* will have a dawn song of whistled notes.

GEOGRAPHICAL VARIATION: No evidence in my samples suggest that there is geographical variation in any of the vocal characters of *M. apicalis*.

ITINERARY OF FIELDWORK

All localities are in Colombia.
1973—March 15-19, near Neiva, Huila; March 22,



FIG. 43. Habitat of *Myiarchus apicalis*. *Top*: Arid tropical zone in the Dagua valley, Valle, Colombia, April 1974; elevation 600 m. *Bottom*: Deciduous, riparian woodland along a tributary of the Río Magdalena, Huila, Colombia, March 1973; elevation 425 m. Sympatric with *M. p. panamensis* at this locality.

near Cali, Valle; March 23-26, near Dagua,
Valle; March 30 through April 1, near
Popayán, Cauca.

1974—April 15-18, and 26, near Dagua again; April

16, near Cali again; April 22-24, near Neiva
again.

1976—January 26-29, near Dagua and Cali again;
March 1-3, near Dagua and Cali again.

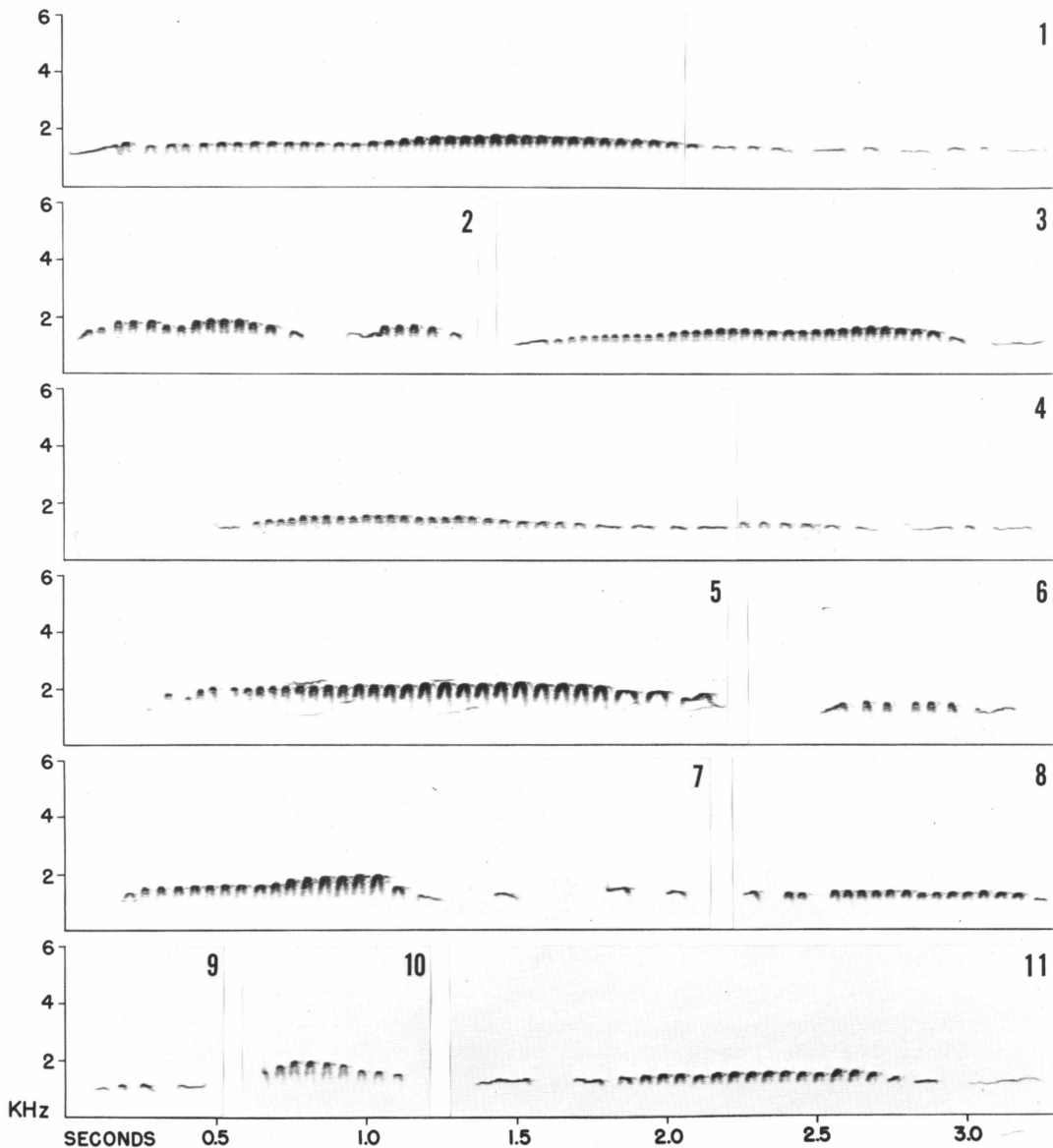


FIG. 44. Variation in vocal characters of *Myiarchus apicalis*: rolls. These spectrograms were made with 45 Hz. filter and are from recordings made in Colombia (1-6, Valle; 7, Cauca; 8-11, Huila).

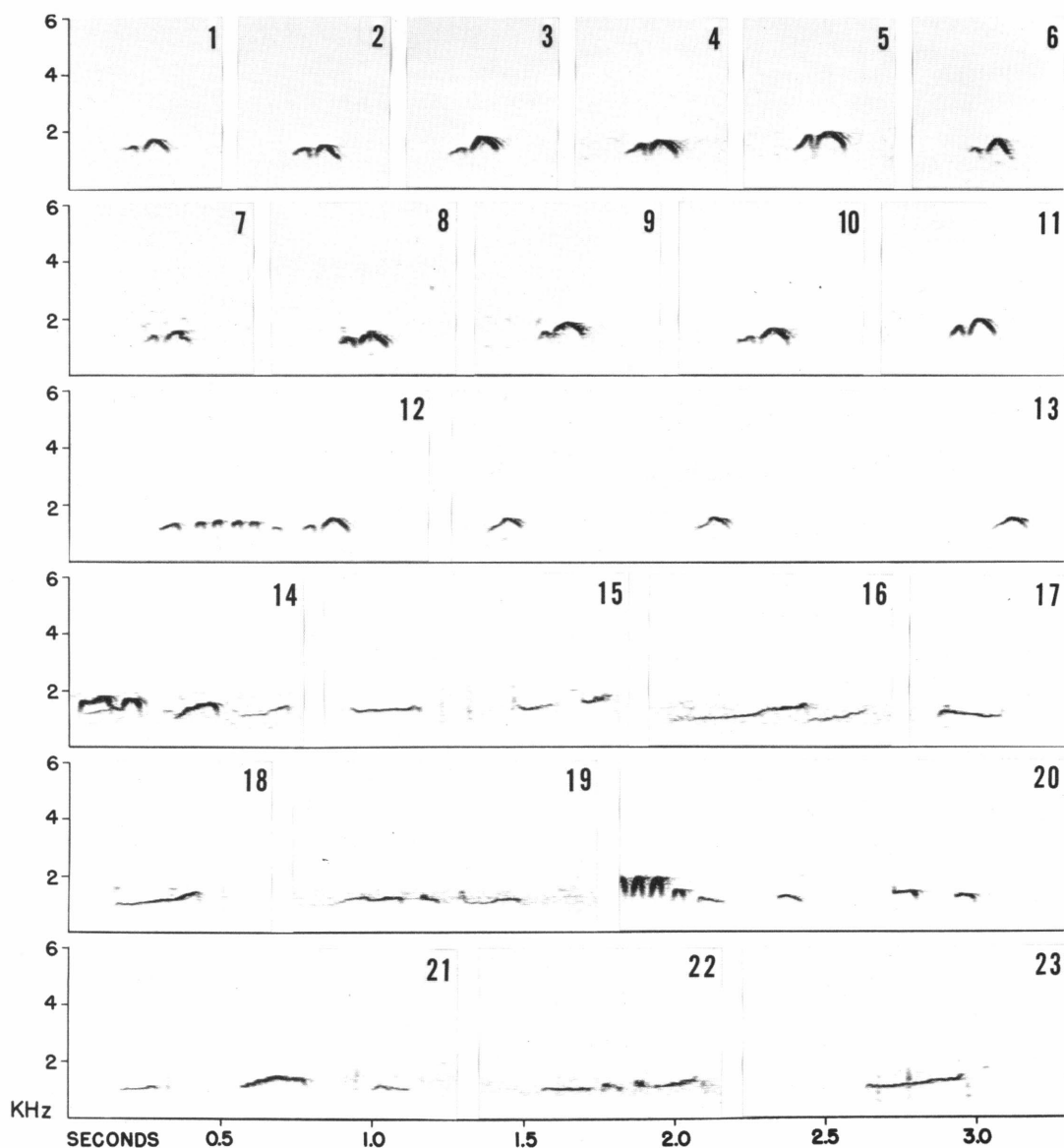


FIG. 45. Variation in vocal characters of *Myiarchus apicalis*: hiccups (1-11), short roll (12), "huit" notes (13), and whistles (14-23). These spectrograms were made with 45 Hz. filter and are from recordings made in Colombia (1-6, 14-19, Valle; 20, Cauca; 7-13, 21-23, Huila).

SYSTEMATICS

Myiarchus apicalis Sclater and Salvin

Myiarchus apicalis Sclater and Salvin, 1881, p. 269
(type locality, "Bogotá," Colombia; co-types in

British Museum [Nat. Hist.]). Berlepsch, 1907, p. 477. Chapman, 1917, p. 476. Todd, 1922, p. 207 (synonymy). Hellmayr, 1927, p. 180 (synonymy). Zimmer, MS. Meyer de Schauensee, 1950, p. 827; 1966, p. 350.

TABLE 32
Measurements (in Millimeters and Grams) in Samples of *Myiarchus apicalis*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	32	88 - 97	92.7 $\pm$ 0.48	2.69	2.91
Females	21	85 - 93	88.5 $\pm$ 0.49	2.23	2.52
Tail Length					
Males	30	81 - 93	87.6 $\pm$ 0.58	3.16	3.60
Females	20	80 - 89	84.4 $\pm$ 0.55	2.44	2.89
Body Weight					
Males	11	26.0 - 33.5	29.6 $\pm$ 0.70	2.33	7.88
Females	12	26.5 - 30.2	28.8 $\pm$ 0.32	1.10	3.82

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 46): There appear to be two disjunct populations in west central Colombia, centering upon the upper Cauca and upper and middle Magdalena valleys, respectively. The Cauca valley population extends northward through the Department of Valle and crosses over the drier passes in the Western Andes northwest of Cali into the upper portion of the Dagua Valley. To the south the species extends beyond the headwaters of the Río Cauca and down into the upper reaches of the Río Patía. In the Magdalena valley the species is known from the Department of Huila in the south to the Department of Santander in the north. Taken at elevations up to 2100 m.

This species is sympatric with *M. tuberculifer* in the Cauca valley, particularly in the lower subtropical zone, and with *M. panamensis* in the middle and upper Magdalena valley; probably only rarely, if at all, sympatric with *M. cephalotes*, which is found at higher elevations.

Specimens examined, 103; localities, from north to south and west to east (see fig. 46; asterisks denote author's study areas): COLOMBIA, El Pescado, Antioquia; San Gil, Santander; Honda, Tolima; Chicoral, Tolima; *Cali, Valle (Dagua; Caldas; Atuncela; San Antonio; Yumbo; Pavas; Jiménez; La María; Bitaco; La Cumbre; Lomitas); *Neiva, Huila; *Popayan, Cauca; Buenavista, Huila (La Plata); San Agustín, Huila; Ancuya, Nariño.

MYIARCHUS PHAEOCEPHALUS SCLATER

The known range of this well-marked South American endemic is limited to the coastal

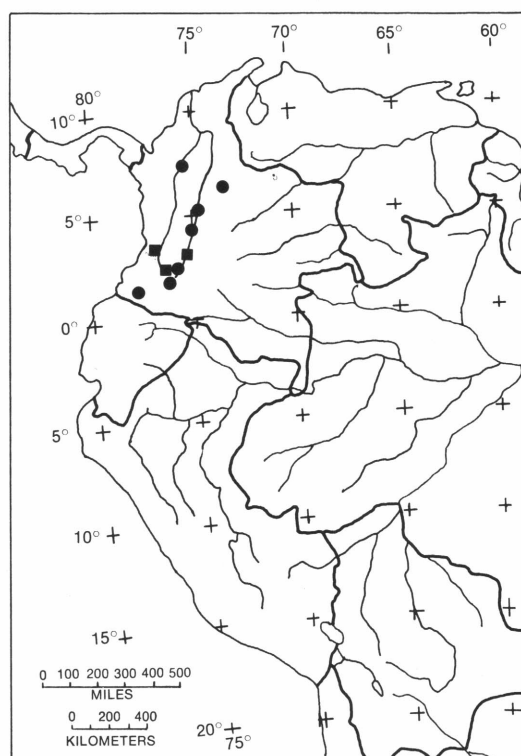


FIG. 46. Distribution of *Myiarchus apicalis* as indicated by localities of specimens examined (circles) and of sites where author studied this taxon in the field (squares). See page 539 for a list of these localities and page 535 for an itinerary of author's fieldwork with this taxon.

plain of Ecuador, and to northwestern Peru, and hence is one of the most restricted geo-

graphic ranges of any species in the genus (fig. 53). The species is nonmigratory. Two subspecies, *phaeocephalus* and *interior*, are admitted here.

DIAGNOSIS: Crown gray anteriorly, becoming darker posteriorly, thereby strongly contrasting with lighter back. Rectrices of adults not marked with Antique Brown. Outer vane of outer rectrix somewhat paler than inner vane. In fresh specimens, entire mandible black, without seasonal or geographical variation, but paling occurs, rendering character unreliable in older museum specimens. Color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics consists of rasping whistles with frequencies as low as 1 and 2 kHz., but *no* rolls or "huit" notes. Dawn song consists of a series of whistles in which an introductory more prolonged whistle is followed in rapid succession by a number of shorter whistles on a scale of slightly decreasing frequency.

HABITAT (FIG. 47): Tropical zone. Clearings in and borders of arid and semiarid deciduous woodland, from sea level up to 1500 m. in the Marañón valley. The Andean range that separates the Pacific drainage from that of the Río Huancabamba (a tributary of the Río Marañón) in northern Peru is apparently sufficiently mesic and high (the pass at Porculla is at 2100 m.) to separate the two subspecies.

BREEDING AND ANNUAL CYCLE: I found two nests of *M. phaeocephalus*, and both were typical *Myiarchus* in site and lining. I know of no reference in the literature to the breeding habits of this species, and the following may be the first published descriptions of the nests and eggs.

The first nest was in a natural cavity formed by a broken-off limb of a mesquite tree (*Prosopis* sp.), in open, rather dry deciduous woodland 43 km. northeast of Sullana, Department of Piura, Peru, on February 28, 1973 (fig. 48). The cavity entrance was 1.7 m. from the ground, and the nest itself was 46 cm. in from the entrance. The nest was constructed largely of goat fur, bits of thin, translucent plastic, pieces of snakeskin, cloth, and a few feathers; it contained three eggs with embryos about 10

days old. The eggs are indistinguishable from those of *Myiarchus crinitus* in size, shape, color, and markings.

A second nest was located 2 m. from the ground in the trunk of a dead mesquite tree, in open, deciduous woodland near Huaquillas, Department of El Oro, Ecuador, on February 22, 1976. The nest was about 30 cm. below the entrance of the natural cavity, and contained a full clutch of three eggs (fig. 49). The nest lining contained feathers, fur, plastic, and shed reptilian skin. The eggs, though not collected, appeared to be similar to those taken from the Peruvian nest.

The limited evidence available suggests that the species breeds from February to April. In addition to the observations above, there is a specimen (AMNH 124703) from Ecuador, dated February 28, that had enlarged testes. The male I collected at the Peruvian nest site (AMNH 822408) had testes that measured 12 by 5 mm., whereas two males taken in August had testes that varied in size from 2 to 3 mm. by 1 to 2 mm. The earliest dated juvenal that I have seen was taken on April 9.

Sixteen specimens showing active molt of the remiges are dated from early May through mid-July.

VOCAL CHARACTERS: The analysis of vocal characters of *M. phaeocephalus* is based on recordings from these samples:

M. p. phaeocephalus—Peru, two pairs; Ecuador, seven pairs

M. p. interior—none

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 50-52.

In response to playback, or when excited by intruding conspecifics, *M. phaeocephalus* vocalizes with repeated hiccups, rasping whistles, and high-pitched whistles. The hiccup in this species (fig. 50:1-12) normally is a two-syllabled call, in which each syllable is a modified "huit." The accent is on the first syllable, by virtue of its greater amplitude and frequency excursion. There is considerable variation in the trace, however; occasionally the energy in the two syllables is continuous, and the first

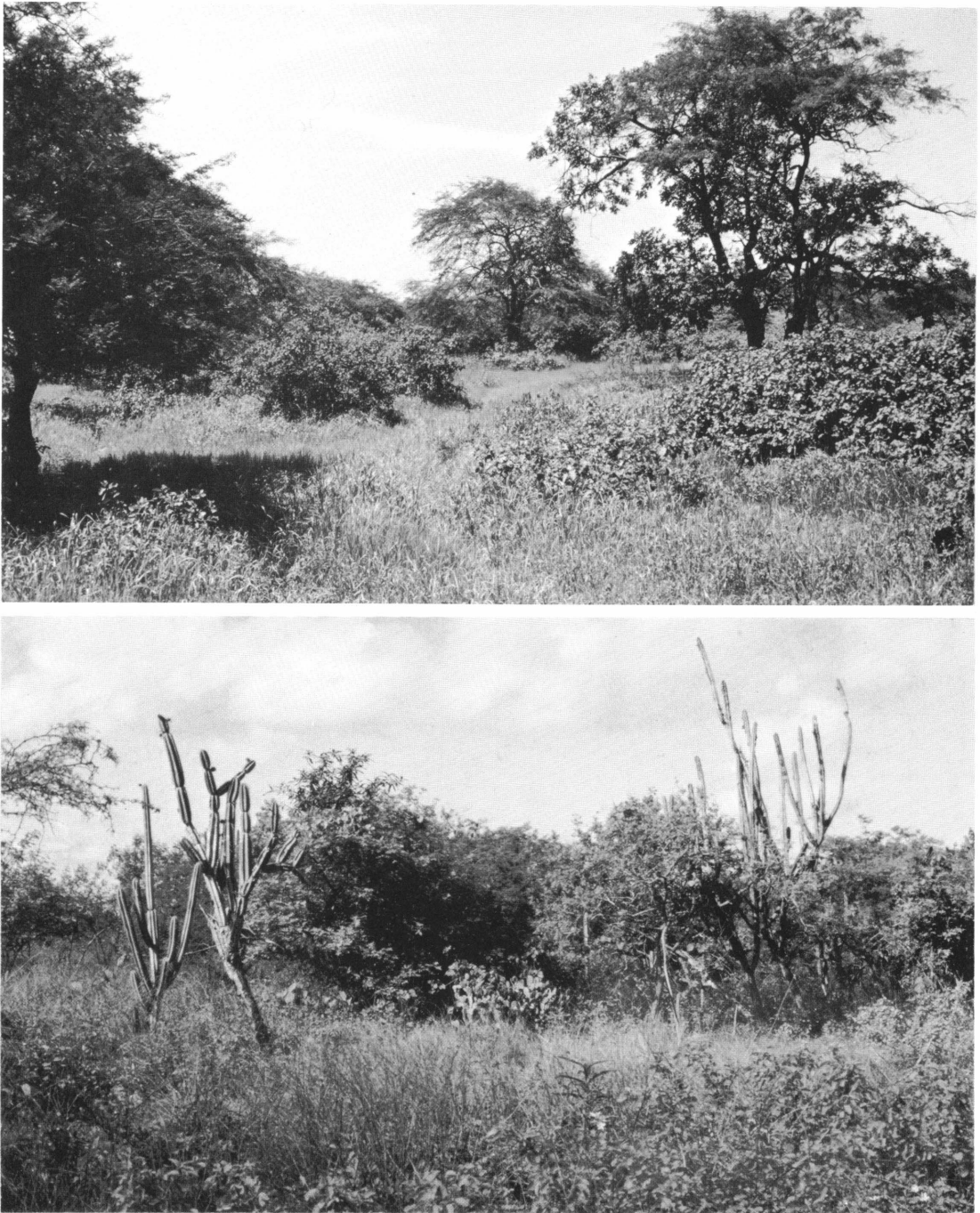


FIG. 47. Habitat of *Myiarchus phaeocephalus phaeocephalus*. *Top*: Open, deciduous woodland 43 km. NE of Sullana, Piura, Peru, February 1973; elevation 150 m. Nest cavity located here, and illustrated in figure 48. *Bottom*: Arid, deciduous woodland in tropical zone of southwestern Ecuador, near Huaquillas, El Oro, February 1976; elevation 25 m. Nest cavity located here, and illustrated in figure 49.



FIG. 48. Nest of *Myiarchus phaeocephalus phaeocephalus* located in habitat illustrated in figure 47, top. Female was incubating three eggs on February 28, 1973. Note presence of hair, feathers, and shed snakeskin in lining removed from nest cavity (bottom). See text.

syllable may be modulated slowly as a vibrato. The rasping whistle (fig. 51:4, and fig. 50:12-24, 26, 28) owes its rasping quality to a modulating frequency of 45 to 60 Hz. Although similar to the rasping whistles of some congeners with respect to the modulating frequency, this call in *M. phaeocephalus* is at a lower frequency (2 kHz. or lower). It may be given as an isolated note, or in a phrase of similar notes, or in close association with a hiccup or series of whistles. A diagnostic feature of this vocal response to playback is the periodic inclusion of single, whistled notes (fig. 51:3). These are relatively high-pitched (3 kHz.) and have a piercing, rather than plaintive, quality. If a roll is included (fig. 50:25, 27), it is short, with only a few "huit"-like components. The absence of prominently featured rolls in this vocal response is diagnostic.

Foraging birds not excited by playback or intruding conspecifics give a series of whistles, delivered in a rapid sequence and in a gradually descending frequency scale (as in fig. 51:5). The introductory whistle in such a series is normally much longer than the others, and can be as long as 1.0 second. In addition to descending in frequency, the series is characterized by a gradual decrease in amplitude as well. Presumably these calls serve as location notes in the communication between paired birds.

DAWN SONG: The dawn song of male *M. phaeocephalus* consists of the same series of whistles as given by foraging birds during the daylight hours (fig. 52), differing only in the constant frequency with which it is delivered per unit time. As in the daytime, the introductory whistle is normally higher pitched and of greater amplitude, hence somewhat piercing in quality, whereas the remaining whistles in the series become progressively more plaintive as they decrease in frequency and amplitude.

GEOGRAPHICAL VARIATION: I have no evidence in my samples to suggest geographical variation in any of the vocal characters of *M. p. phaeocephalus*. I have had no field experience with *M. p. interior*.

ITINERARY OF FIELDWORK

1973—February 25-28, with *phaeocephalus* near

Chilaco, Piura, Peru (43 km. NE of Sullana). 1976—January 31 through February 5, with *phaeocephalus* near Huaquillas, El Oro, Ecuador (and also Santa Rosa and Arenillas); February 22-23, with *phaeocephalus* near Huaquillas again; February 24-27, with *phaeocephalus* near Manta, Manabí, Ecuador.

SYSTEMATICS

Myiarchus phaeocephalus phaeocephalus
Sclater

Myiarchus phaeocephalus Sclater, 1860b, p. 281



FIG. 49. A female *Myiarchus phaeocephalus phaeocephalus* about to enter her nest cavity in trunk of a dead *Prosopis*, where she was incubating a clutch of three eggs on February 22, 1976. Photograph taken with a 300 mm. lens, without a blind, near Huaquillas, El Oro, Ecuador. Habitat at this locality is illustrated in figure 47, bottom.

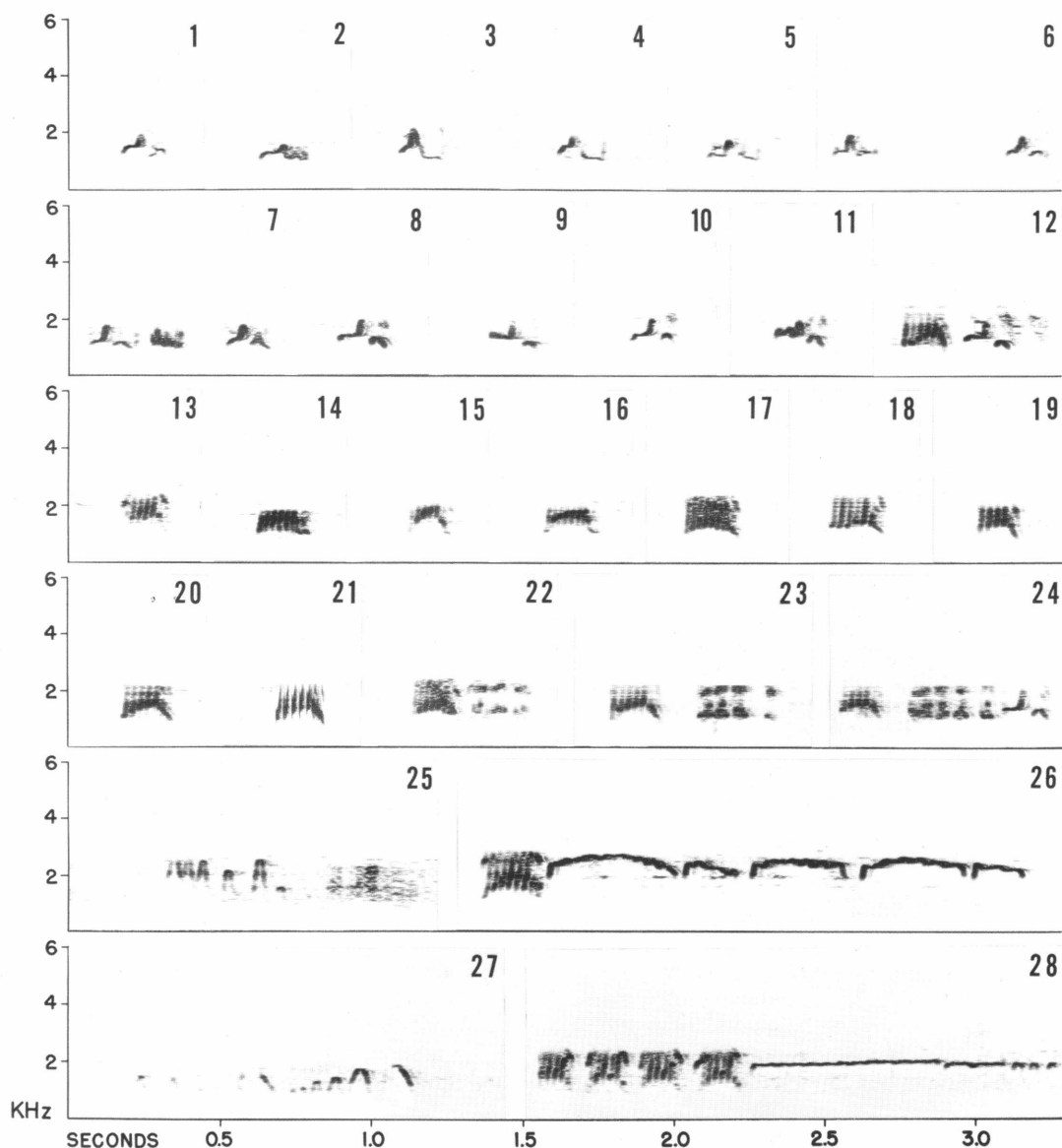


FIG. 50. Variation in vocal characters of *Myiarchus phaeocephalus*: hiccups (1-11), rasping whistles (12-24), and short rolls (25, 27). Spectrograms were made from recordings of *M. p. phaeocephalus* in Ecuador (1-7, 13-17, 22, 26-28) and Peru (8-12, 18-21, 23-25). 300 Hz. filter was used for 21 only.

(type locality, Babahoyo, Ecuador; cotypes in the British Museum [Nat. Hist.]). Taczanowski, 1884, p. 323. Berlepsch, 1907, p. 477. Todd,

1922, p. 208. Chapman, 1926, p. 528. Hellmayr, 1927, p. 174 (synonymy). *Myiarchus ferox phaeocephalus*: Ridgway, 1907, p.

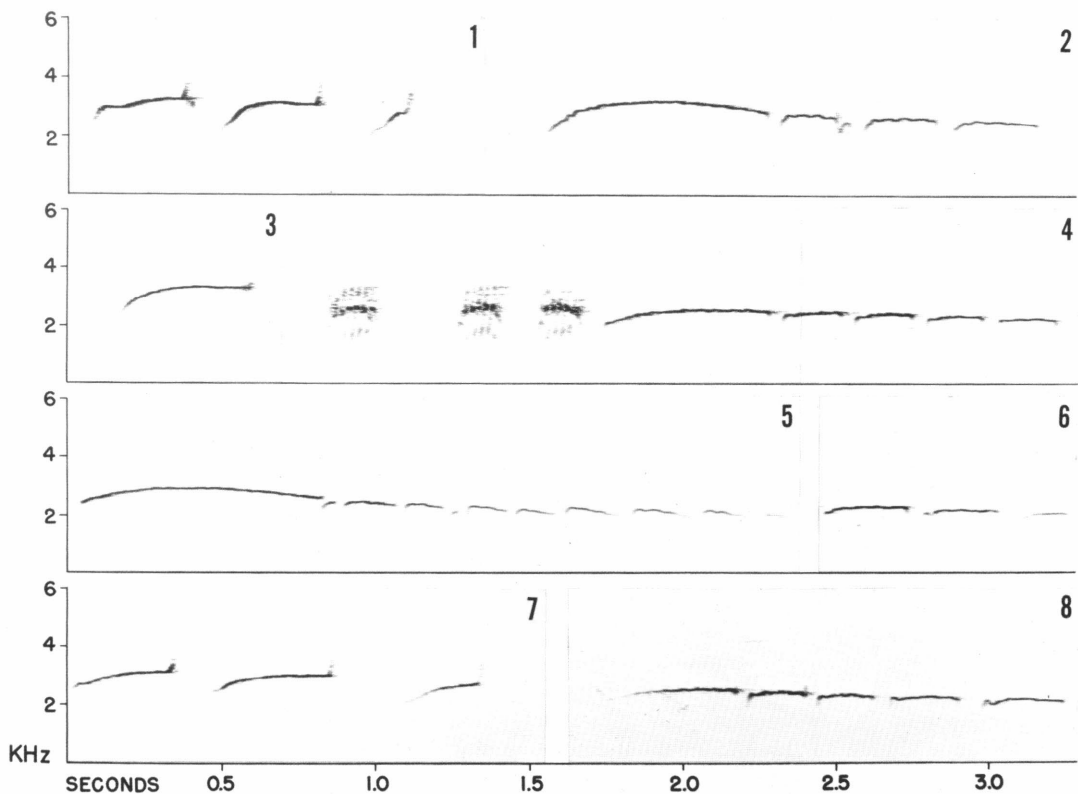


FIG. 51. Variation in vocal characters of *Myiarchus phaeocephalus*: whistles and whistle series. Spectrograms were made with 45 Hz. filter and are from recordings of *M. p. phaeocephalus* in Ecuador (1-5, 8) and Peru (6, 7).

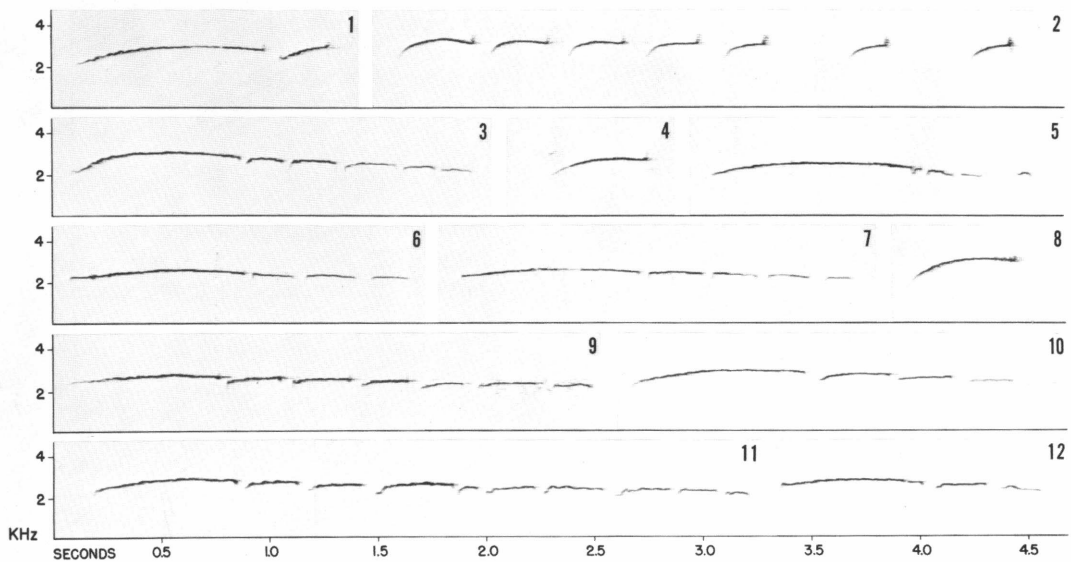


FIG. 52. Variation in vocal characters of *Myiarchus phaeocephalus*: dawn song. Spectrograms were made with 45 Hz. filter and are from recordings of *M. p. phaeocephalus* in Ecuador (1-7) and Peru (8-12).

612 (new combination). Oberholser, 1918, p. 306. Bangs and Noble, 1918, p. 455 (in part).

Myiarchus toddi Chapman, 1923, p. 10 (type locality, Palambla, Peru; holotype in the American Museum of Natural History, examined). Hellmayr, 1927, p. 175.

Myiarchus phaeocephalus phaeocephalus: Zimmer, 1938a, p. 9. Bond, 1947, p. 138.

DIAGNOSIS: Crown and back slightly darker and grayer, abdomen somewhat paler than in *interior*; wing length averages slightly greater than in *interior* (table 33).

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 53): Western Ecuador (Esmeraldas southward) and northwestern Peru (Departments of Tumbes and Piura). If the unique specimen of "*toddi*" is considered but an individual variant of *phaeocephalus*, deficient in yellow pigmentation as suggested by Hellmayr (1927, p. 175), then the collecting locality, Palambla, represents the southernmost record in Piura. Now isolated geographically from *interior*.

Sympatric with *M. tuberculifer* in Ecuador, and perhaps locally with *M. semirufus* in Peru.

Specimens examined, 66; localities, by country, from north to south (see fig. 53; asterisks denote author's study areas): ECUADOR, Esmeraldas, Esmeraldas; Chone, Manabí (Machalilla; Bahía); *Manta, Manabí; Quevedo, Los Ríos (Mantequilla); Guayaquil, Guayas (Daule; Milagro; Chongónquito); Isla de Puná, Guayas; *Huaquillas, El Oro (Santa Rosa; Arenillas; Piedras); Sabianga, Loja (Cruzpamba). PERU, *Chilaco, Piura (Paletillas; Romero); Palambla, Piura.

Myiarchus phaeocephalus interior Zimmer

Myiarchus phaeocephalus interior Zimmer, 1938a, p. 9 (type locality, Perico, Río Chinchipe, Peru; holotype in the American Museum of Natural History, examined). Bond, 1947, p. 138.

DIAGNOSIS: Crown and back slightly browner, and abdomen slightly richer yellow than in the nominate form; wing length averages slightly less than in nominate *phaeocephalus* (table 33).

DISTRIBUTION AND SPECIMENS EXAMINED

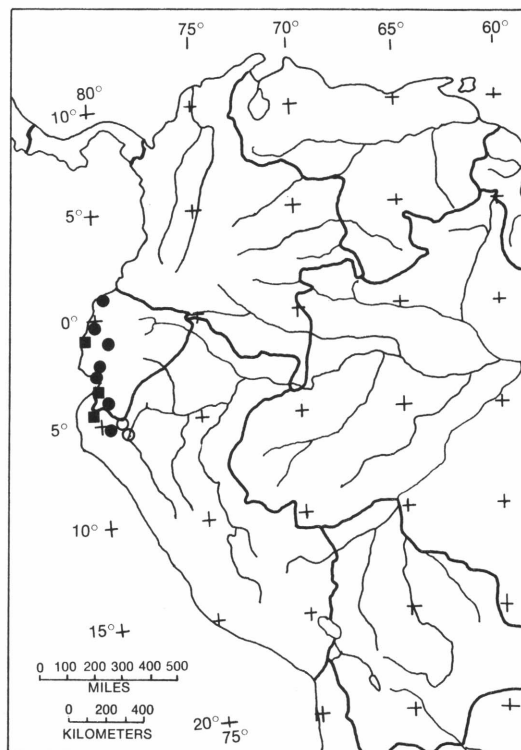


FIG. 53. Distribution of *Myiarchus phaeocephalus phaeocephalus* (solid circles and squares) and of *M. p. interior* (open circles) as indicated by localities of specimens examined (circles) and by sites where author studied the species in the field (squares). See page 549 for lists of these localities and page 543 for an itinerary of author's fieldwork with this species.

(FIG. 53): The drainage of the Río Marañón in northern Cajamarca and northwestern Amazonas, Peru. Isolated geographically from *phaeocephalus*.

Sympatric locally with *M. tyrannulus*, *M. ferox*, and *M. tuberculifer*.

Specimens examined, 29; localities, from north to south (see fig. 53): PERU, Cajamarca (Río Chinchipe; San Ignacio; Huarandosa; Charapi); Jaén, Cajamarca (Bellavista; Pucará; Loma Santa; Bagua, Amazonas; Río Tamborapa).

TABLE 33
Measurements (in Millimeters and Grams) in Samples of *Myiarchus phaeocephalus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. p. phaeocephalus</i>					
Wing Length					
Males	30	90 - 98	94.1 ± 0.39	2.16	2.29
Females	22	86 - 94	90.3 ± 0.45	2.10	2.32
Tail Length					
Males	29	80 - 94	88.1 ± 0.62	3.36	3.82
Females	20	79 - 90	85.6 ± 0.74	3.32	3.87
Body Weight					
Males	5	26.5 - 30.0	28.7 ± 0.62	1.38	4.80
Females	2	27.5 - 30.1	28.8 —	—	—
<i>M. p. interior</i>					
Wing Length					
Males	13	89 - 93	91.0 ± 0.30	1.08	1.19
Females	9	85 - 93	87.7 ± 0.91	2.74	3.12
Tail Length					
Males	12	86 - 91	88.9 ± 0.45	1.56	1.76
Females	9	81 - 93	85.7 ± 1.22	3.67	4.29
Body Weight					
Males	6	24.9 - 27.0	25.9 ± 0.40	0.98	3.78
Females	1	—	28.0 —	—	—

MYIARCHUS CEPHALOTES TACZANOWSKI

This South American endemic is found throughout the subtropical and lower temperate zones of the Andes, from Bolivia to Venezuela, and in the northern coastal range of Venezuela (fig. 58). The species is polytypic, with two subspecies admitted here, *cephalotes* and *caribbaeus*, neither of them migratory. Zimmer's *caucae* and *gularis* are placed in synonymy with *cephalotes*.

DIAGNOSIS: One of the larger (see measurements in tables 34 and 35) "dark-tailed" species, i.e., rectrices of adults not conspicuously marked with Antique Brown. Outer pair of rectrices with outer vanes whitish and noticeably paler than inner vanes. Greater and median upper wing coverts broadly tipped with whitish. Coloration of crown uniform throughout and not noticeably contrasting with that of back. Tail long, relative to wing: ratio of tail length to wing length usually 95 percent or more and rarely less than 93 percent. Wing rounded: fifth primary usually equal to or longer than the

ninth (up to 5 mm. longer) and rarely as much as 1 or 2 mm. shorter than the ninth; fourth primary usually at least 6 mm. longer than the tenth (up to 13 mm. longer) and rarely less than 5 mm. longer than the tenth. In fresh specimens, entire mandible black, with no seasonal or geographical variation; but paling with age, rendering the character unreliable in older museum specimens. Color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics consists of repeated rasps, rasp-whistles, and series of descending whistles, but *no* rolls. Dawn song consists solely of sharp whistles.

HABITAT (FIGS. 6 AND 54): Forests and open woodlands of the subtropical and lower temperate zones; recorded at elevations of 800 to 2200 m. in Bolivia, 800 to 3000 m. in Peru, 1500 to 3000 m. in Colombia, and 1500 to 2200 m. in Venezuela.

BREEDING AND ANNUAL CYCLE: I know of no reference in the literature to breeding behav-



FIG. 54. *Top*: Habitat of *Myiarchus cephalotes caribbaeus* in humid forest of subtropical zone near Colonia Tovar, Aragua, Venezuela, May 1968; elevation 2000 m. *Bottom*: Habitat of *M. c. cephalotes* in humid forest of subtropical zone near San Ramón, Junín, Peru, November 1972; elevation 1800 m. Sympatric with *M. tuberculifer atriceps* at this locality.

ior in this species. My only observation was made near Popayán, Colombia, on May 9, 1974, when I watched a bird gathering plant fibers until it had a full bill and flew out of sight. A few minutes later I found an individual peering into a natural cavity in a tree, and in the same direction as that taken by the bird I

saw earlier carrying nesting material. The use of this cavity as a nest site was not confirmed.

The breeding season in Colombia and Venezuela is from April through June. Males taken in late April and early May had their testes fully enlarged (up to 10 by 5 mm.), and females taken in early May had the oviduct

TABLE 34
Measurements (in Millimeters and Grams) in Samples of *Myiarchus cephalotes cephalotes*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	70	86 - 100	93.3 ± 0.29	2.43	2.60
Females	64	84 - 94	87.6 ± 0.26	2.04	2.33
Tail Length					
Males	73	83 - 95	90.1 ± 0.32	2.74	3.03
Females	65	81 - 89	85.0 ± 0.26	2.14	2.51
Body Weight					
Males	6	27.5 - 31.5	29.5 —	—	—
Females	7	26.0 - 29.5	27.8 —	—	—
Bill Length					
Males	73	11.8 - 14.5	13.10 ± 0.06	0.502	3.83
Females	61	10.5 - 13.9	12.40 ± 0.07	0.568	4.58
Fourth Primary — Tenth Primary					
Males	59	+4 to +13	+8.6 ± 0.23	1.77	20.73
Females	52	+4 to +13	+8.6 ± 0.23	1.68	19.47
Fifth Primary — Ninth Primary					
Males	60	-2 to +3	+0.9 ± 0.15	1.16	133.49
Females	51	-1 to +4	+0.9 ± 0.13	0.96	111.19

TABLE 35
Measurements (in Millimeters and Grams) in Samples of *Myiarchus cephalotes caribbaeus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	30	81 - 91	87.3 ± 0.41	2.24	2.57
Females	21	78 - 86	81.8 ± 0.47	2.14	2.61
Tail Length					
Males	29	80 - 91	85.9 ± 0.44	2.39	2.78
Females	21	77 - 86	81.8 ± 0.43	1.99	2.43
Body Weight					
Males	3	22.5 - 27.5	24.3 —	—	—
Females	4	23.0 - 24.5	23.9 —	—	—
Bill Length					
Males	30	11.6 - 13.3	12.43 ± 0.09	0.496	3.99
Females	21	11.0 - 12.9	11.83 ± 0.12	0.536	4.53
Fourth Primary — Tenth Primary					
Males	16	+5 to +11	+8.6 ± 0.39	1.55	18.08
Females	12	+8 to +12	+10.0 ± 0.41	1.41	14.14
Fifth Primary — Ninth Primary					
Males	16	0 to +4	+1.3 ± 0.30	1.20	91.01
Females	12	0 to +5	+2.5 ± 0.51	1.78	71.36

slightly enlarged and ova up to 2 mm. in diameter. The three juvenals that I have seen from these northern populations were taken between late April and mid-May. Specimens with active molt of the remiges have been taken between late June and late October. An incomplete pre-alternate molt occurs in March, about two months prior to the breeding season (Lanyon, 1975b).

I have no comparable breeding date for the southern populations, but one might expect this montane form to breed at approximately the same time as *Myiarchus tuberculifer atriceps*, with which it is sympatric. Presumably, as in the montane populations of *M. tuberculifer*, there is a gradual shift in the annual cycle of *M. cephalotes* in northern Peru and Ecuador, though there are very few data at hand. Specimens showing active molt of remiges have been taken in Peru and Bolivia from November through April. I have seen three juvenals taken in Peru in late January and early February.

VOCAL CHARACTERS: The analysis of vocal characters of *M. cephalotes* is based on recordings from these samples:

M. c. caribbaeus—Venezuela, nine pairs

M. c. cephalotes—Peru, two pairs; Colombia, seven pairs

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 55-57.

In response to playback, or when excited by intruding conspecifics, *M. cephalotes* vocalizes with a characteristic series of descending whistled notes, rasps, rasp-whistles, and hiccups (nominate subspecies only). In the series of whistles (fig. 55), the introductory whistle is normally sharp and piercing, but the remaining whistles become progressively more plaintive as they drop in frequency, amplitude, and frequency excursion. This series of whistles is often followed immediately by some rasps. The rasp (fig. 56:7-18) of this species has a modulating frequency close to 100 cycles per second, is often prolonged to nearly a full second in length, and is noisier than the comparable calls of most species of *Myiarchus* due to the great deviation from the carrier frequency. It may be given as an isolated call or in a series of similar notes in rapid sequence. Occasionally the carrier frequency of a rasp will continue with

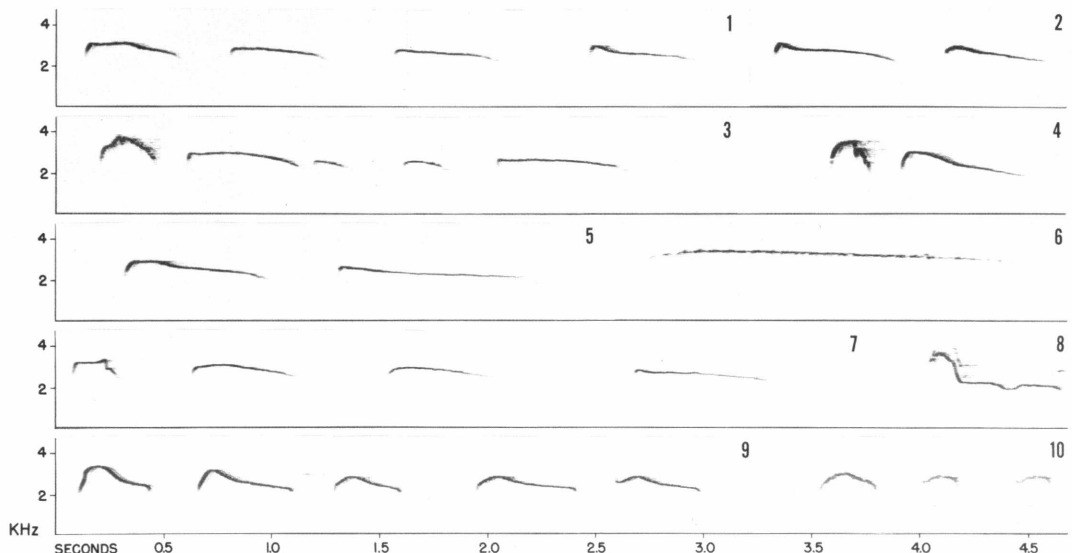


FIG. 55. Variation in vocal characters of *Myiarchus cephalotes*: series of descending whistles. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. c. caribbaeus* (Venezuela, 1-7); *M. c. cephalotes* (Peru, 8; Colombia, 9, 10).

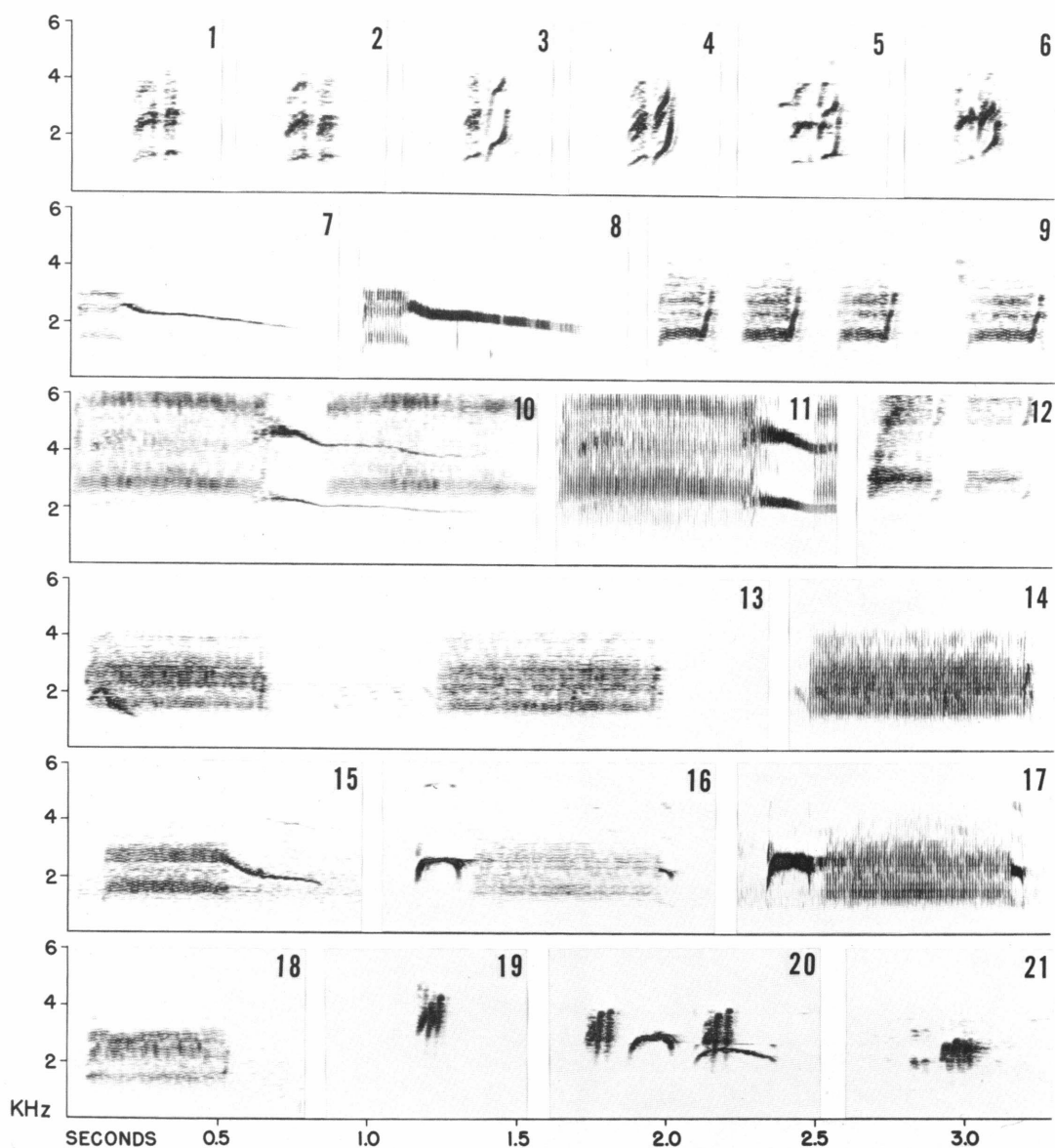


FIG. 56. Variation in vocal characters of *Myiarchus cephalotes*: hiccups (1-6), rasp-whistles (7, 8, 10, 11), rasps (7-18) and rasping whistles (19-21). Spectrograms were made from recordings of the following populations: *M. c. caribbaeus* (Venezuela, 7-15, 19, 20); *M. c. cephalotes* (Colombia, 1-6, 16-18, 21). The 300 Hz. filter was used for 8, 11, 14, and 17 only.

virtually no modulation for a period of 0.5 second or longer. These rasp-whistles (fig. 56: 7, 8, 10, 11) demonstrate the continuum of a common carrier frequency. The nominate sub-

species has an additional call, the hiccup (fig. 56:1-6), as part of its vocal response to playback. It is a call of two syllables, with the accent on the second syllable by virtue of a

greater frequency excursion and amplitude. The occasional rasping whistle, with a modulating frequency of about 30 Hz. (fig. 56:19-21), and a short roll (fig. 57: 15-21) may also be included, but these calls are not prominent features of this vocal response. Figure 57:18 illustrates how the carrier frequency may be modulated to a vibrato, not common in the repertoire of this species but characteristic of other species of the genus.

Foraging birds not excited by playback or intruding conspecifics will deliver an occasional sharp, piercing whistle (fig. 57:1-10). These are isolated calls, given at intervals of many seconds, and presumably serve as location notes in the communication between paired birds. They owe their quality to their high frequency (3 to 4 kHz.), short duration (less than 0.25 second), amplitude, and great frequency excursion.

DAWN SONG: The dawn song of male *M. cephalotes* consists exclusively of the same sharp, piercing whistles that serve as location notes during daylight hours (fig. 57:1-10). The only feature of the dawn song distinguishing it from the daytime renditions is the constant frequency with which it is delivered per unit time. The time interval between the whistles of dawn song is variable but usually more than 5 seconds.

GEOGRAPHICAL VARIATION: The only geographical variation in vocalizations demonstrable in my samples is the absence of the hiccup in *caribbaeus* of Venezuela. No hiccups were recorded from any of the nine pairs of *caribbaeus* with which I worked, though in each case I provoked and received extensive vocal response to playback. By way of contrast, all five pairs of Colombian *cephalotes*, for which I have comparable samples of recordings, frequently rendered hiccup notes in response to playback.

ITINERARY OF FIELDWORK

- 1968—May 5-7, with *caribbaeus* near Colonia Tovar, Aragua, Venezuela.
 1969—May 17-19, with *caribbaeus* near Colonia Tovar again.
 1972—November 11, with *cephalotes* near San Ramón, Junín, Peru.
 1973—March 9-13, and March 30-31, with *cephalotes* near Popayán, Cauca, Colombia.

- 1974—April 18-20, and May 9-11, with *cephalotes* near Popayán again; April 28 through May 1, with *caribbaeus* near Colonia Tovar again; May 3-4, with *caribbaeus* near Cubíro, Lara, Venezuela.

SYSTEMATICS

Myiarchus cephalotes cephalotes Taczanowski

Myiarchus cephalotes Taczanowski, 1879, p. 671 (type locality, Tambillo, Peru; holotype formerly in Warsaw, now lost according to Zimmer, 1938a, p. 15). Chapman, 1917, p. 476. Todd, 1922, p. 206 (synonymy).

Myiarchus cephalotes cephalotes: Chapman, 1926, p. 527. Hellmayr, 1927, p. 179 (synonymy). Zimmer, 1938a, p. 15. Bond, 1947, p. 139.

Myiarchus cephalotes cauae Zimmer, 1938a, p. 16 (type locality, Santa Elena, Colombia; holotype, AMNH 133794, examined). Meyer de Schauensee, 1950, p. 826.

Myiarchus cephalotes gularis Zimmer, 1938a, p. 17 (type locality, Locotal, Bolivia; holotype, AMNH 137660, examined). Bond and Meyer de Schauensee, 1942, p. 346. Bond, 1947, p. 139.

DIAGNOSIS: Larger than *caribbaeus* (see measurements in tables 34 and 35). Outer web of outermost rectrix averages darker (more pigmentation).

Vocal response to intruding conspecifics includes hiccup notes.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 58): Known from the Yungas of Bolivia, the slopes of eastern and central ranges of the Andes of Peru, the eastern slopes of the Andes in Ecuador, and extending northward along the central range of the Andes in Colombia. Formerly believed to be absent from the eastern range of the Andes in Colombia, but María and Olivares (1976) have recently reported on specimens from Norte de Santander (south of Cúcuta, near the Venezuelan border) and from Cundinamarca (La Aquadita and Quetame). Not known to be in contact with *caribbaeus* of Venezuela.

Sympatric with *M. tuberculifer* from Colombia to Bolivia, though it favors somewhat higher elevations than that species.

Specimens examined, 169; localities, by country, from north to south (see fig. 58; asterisks denote author's study areas): COLOMBIA, Valdivia, Antioquia (Santa Rosa de

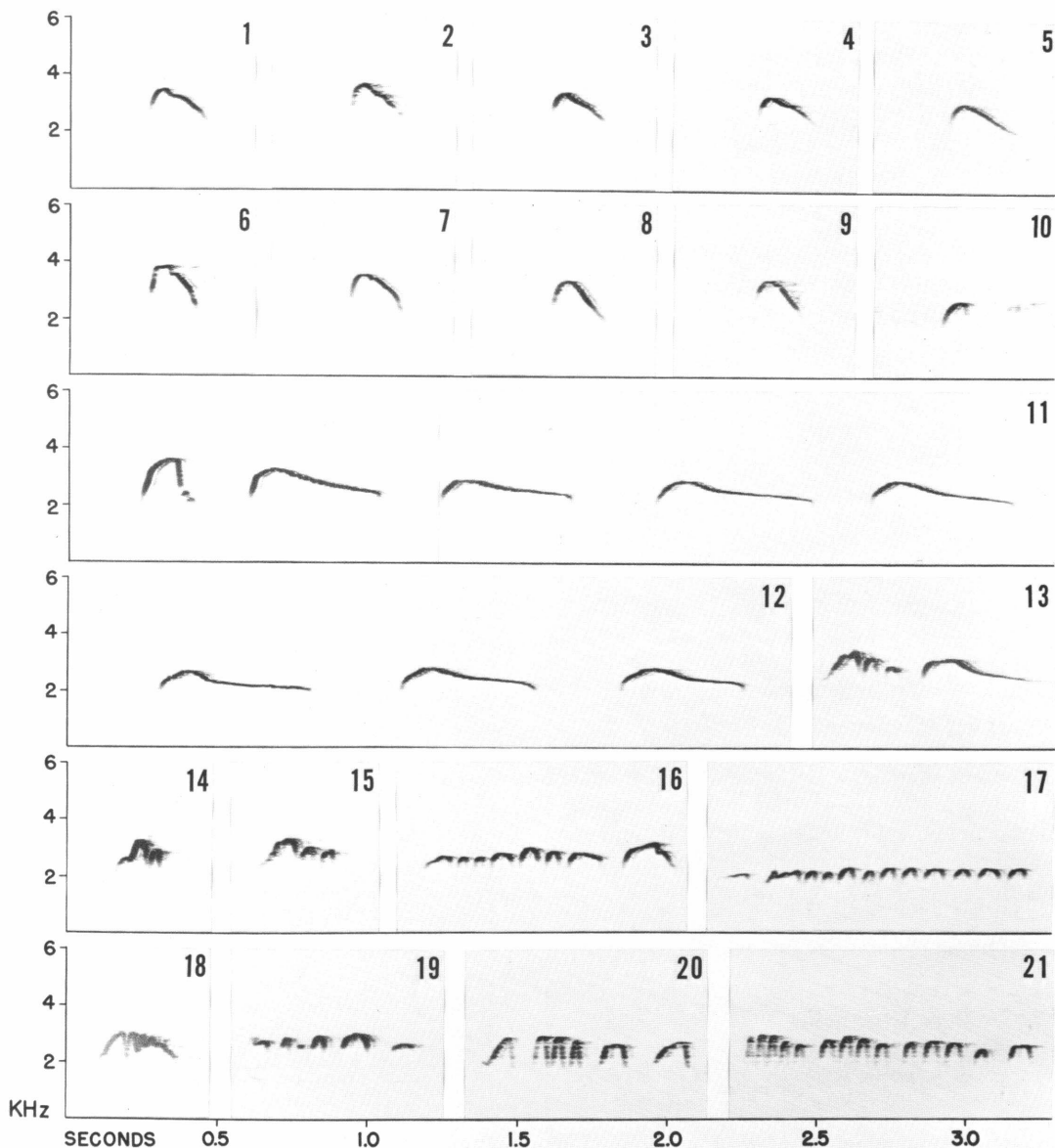


FIG. 57. Variation in vocal characters of *Myiarchus cephalotes*: sharp whistles and dawn song (1-10), series of descending whistles (11-12), and short rolls (13-21). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. c. caribbaeus* (Venezuela, 1-5, 13-17); *M. c. cephalotes* (Peru, 10; Colombia, 6-9, 11, 12, 18-21).

Osos); Frontino, Antioquia (Río Urrao); Santa Elena, Antioquia; Sonsón, Antioquia; Salento, Caldas (El Edén; Quindío; Laguneta; Toche, Tolima); Palmira, Valle; *Popayán, Cauca

(Puracé; Timbío; El Tambo; Cerro Munchique); Buenavista, Huila (Belén); San Agustín, Huila (La Candela; La Palma); Río Rumi-Yacu, Nariño. ECUADOR, Baeza, Napo (Río Oya-

cachi; Sumaco; Puente del Río Quijos); Archidona, Napo; Loja, Loja. PERU, Chaucabamba (Tabaconas); Moyobamba, San Martín (Uchco); Chachapoyas, Amazonas (Levanto; San Pedro; Leymebamba; Molinopampa); Río Jelashte, San Martín; Nuevo Loreto, San Martín; Utcubamba, La Libertad; Cerros del Sisa, Loreto; Chinchao, Huánuco (Cushi-Libertad; Vista Alegre; Huachipa); Rumicruz, Pasco; *San Ramón, Junín (Chelpes; Pan de Azúcar; Utcuyacu; Huacapistana; Vitoc; La Oroya); Santo Domingo, Puno. BOLIVIA, Mapiri, La Paz; Yungas, La Paz (Calabatea); Yungas, Cochabamba (Locotal; Roquefalta; Incachaca; Palmar); Vermejo).

REMARKS: As Zimmer (1938a) pointed out, the populations of *M. cephalotes* from Colombia to Bolivia are variable with respect to the extent of pigmentation in the outer web of the outermost rectrices. Those in northern Peru and Ecuador have the darkest outer web, whereas those in Colombia and in Bolivia have the palest outer web and thus approach *caribbaeus* in this character. Most Colombian specimens (Zimmer's *caucaae*) are inseparable from Bolivian specimens (Zimmer's *gularis*), however, and there has been no significant divergence mensurally among these populations, as has occurred with *caribbaeus*. For these reasons, and in the interest of maintaining consistent taxonomic treatment throughout the genus, I prefer not to recognize Zimmer's races.

Myiarchus cephalotes caribbaeus Hellmayr

Myiarchus cephalotes caribbaeus Hellmayr, 1925a, p. 73 (type locality, Cerro del Ávila, Venezuela; holotype, Zoologisches Museum, Munich). Hellmayr, 1927, p. 180 (synonymy). Zimmer, 1938a, p. 19. Phelps and Phelps, 1963, p. 191.

DIAGNOSIS: Smaller than *cephalotes* (see measurements in tables 34 and 35). Outer web of outermost rectrix averaging paler (less pigmentation) throughout.

Vocal response to intruding conspecifics has no hiccup notes.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 58): Known from three separated mountainous regions of northern Venezuela: the Andes of Trujillo and Lara, the northern coastal

range in Aragua and the Distrito Federal, and the mountains of Sucre. Allopatric with *cephalotes* of Colombia.

Sympatric with *M. tuberculifer*, but favoring somewhat higher elevations than that species.

Specimens examined, 57; localities, from west to east (see fig. 58; asterisks denote author's study areas): VENEZUELA, Páramo de Misís, Trujillo (Guamito); *Cubíro, Lara; *Colonia Tovar, Aragua (Maracay; El Junquito, Distrito Federal); Cerro del Ávila, Distrito Federal (Loma Redonda; Ño León); Carapas, Sucre (Cumanacoa; La Guamal; Cerro Turumiquire).

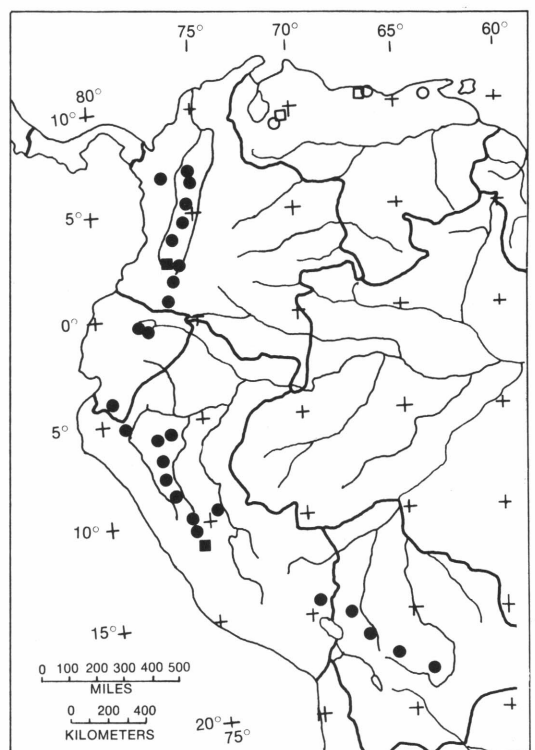


FIG. 58. Distribution of *Myiarchus cephalotes cephalotes* (solid circles and squares) and of *M. c. caribbaeus* (open circles and squares) as indicated by localities of specimens examined (circles) and by the sites where author studied the species in the field (squares). See pages 552 and 554 for lists of these localities and page 552 for an itinerary of author's fieldwork with this species.

TABLE 36
Measurements (in Millimeters) in Combined Samples of Both Subspecies of *Myiarchus cephalotes*

Measurement	N	Range	Mean, S.E.	S.D.	C.V.
Ratio of Tail Length to Wing Length	180	92 - 101	97.4 $\pm$ 0.15	1.99	2.04
Fifth Primary minus Ninth Primary	139	-2 to +5	+1.1 $\pm$ 0.11	1.24	117.06
Fourth Primary minus Tenth Primary	139	+4 to +13	+8.7 $\pm$ 0.15	1.72	19.70

RELATIONSHIP OF
cephalotes AND *caribbaeus*

The two subspecies of *M. cephalotes*, though barely recognizable morphologically compared with those of other species of *Myiarchus*, are of particular interest because of their allopatry and their slight divergence in vocal characters (absence of hiccup notes in *caribbaeus*). My data on response to playback, though not as conclusive and extensive as I would like, suggest that each form will respond to the vocal repertoire of the other but less strongly than to its own repertoire. In 1972 and 1973 I had great difficulty locating pairs of *cephalotes* in Peru and Colombia, using a reconnaissance tape consisting of *caribbaeus* vocal characters. Likewise, when I returned to Venezuela in 1974 with a tape made from my recordings of Colombian *cephalotes* (including the hiccup notes), I found *caribbaeus* to be more responsive generally to its own repertoire than to that of Colombian birds. Two playback experiments conducted with a pair of *caribbaeus* near Colonia Tovar, Aragua, Venezuela, on May 1, 1974, further illustrate this tendency toward a differential response:

Experiment 1—study area one, 1700 m. Tapes used,

Colombian *cephalotes* vs. *M. tuberculifer*. Birds silent, location unknown at start at 9:21 A.M. No show during first half; cable switch at 9:28. One bird calling softly outside experimental area at 9:33, giving descending whistles. Moved into 40 ft. of *cephalotes* model at 9:34, foraging. Both birds at 30 ft. from *cephalotes* model at end of experiment.

Experiment 2—same locality, pair, and date as above. Tapes used, *caribbaeus* vs. *M. apicalis*. Birds had become silent, located 30 ft. above site used for *cephalotes* model in last experiment. Start at 9:38 A.M. Within one minute one bird was giving rasps and descending whistles. Moved to midpoint by 9:40, still calling well. At 9:42, calling from edge of *caribbaeus* area, about 50 ft. from model. Both birds moved into *caribbaeus* area by 9:42:30, calling. To 25 ft. of *caribbaeus* model by 9:43, giving mostly rasps. Then to 20 ft. of model. Both about 20 ft. above *caribbaeus* model at cable switch at 9:45. Remained within 50 ft. of new *apicalis* model until 9:49, when moved to midpoint, giving descending whistles. Both birds to 50 ft. of new *caribbaeus* model by 9:50. One to 30 ft. of model. At 9:50:30, one bird was at 30 ft., the other 40 ft. from *caribbaeus* model, giving rasps and descending whistles. Both at about 30 ft. from *caribbaeus* model at end of experiment. Good response, including re-orientation, to *caribbaeus* tape, in contrast to rather poor response to *cephalotes* in previous experiment.

MYIARCHUS PANAMENSIS LAWRENCE

This species has a rather restricted range in southern Middle America and in western Colombia and Venezuela, west of the easternmost ranges of the Andes (fig. 62). It is polytypic, with two subspecies admitted here, *panamensis* and *actiosus*, neither of them migratory.

The species *panamensis* heretofore has been considered by most workers to be conspecific with *M. ferox*, with *venezuelensis* being re-

garded as the intermediate representative, geographically and morphologically. In this study *M. panamensis* has been found to be specifically distinct from both *M. ferox* and *M. venezuelensis* and to be sympatric with the latter species. Wetmore's *audens* is placed in synonymy with *panamensis*.

DIAGNOSIS: One of the larger (see measurements in tables 37 and 38) "dark-tailed" species, i.e., rectrices of adults not conspic-

TABLE 37
Measurements (in Millimeters and Grams) in Samples of *Myiarchus panamensis panamensis*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	83	90 - 100	93.8 ± 0.21	1.91	2.03
Females	97	83 - 95	89.7 ± 0.23	2.28	2.54
Tail Length					
Males	81	85 - 95	89.1 ± 0.27	2.44	2.74
Females	96	80 - 92	85.4 ± 0.26	2.58	3.02
Body Weight					
Males	6	29.0 - 34.0	31.0 ± 0.92	2.26	7.28
Females	10	27.5 - 38.5	32.1 ± 1.14	3.60	11.22
Fourth Primary minus Tenth Primary					
Males	82	+4 to +11	+6.9 ± 0.19	1.73	25.09
Females	104	+5 to +10	+7.3 ± 0.14	1.47	20.10
Fifth Primary minus Ninth Primary					
Males	81	-3 to +3	+0.3 ± 0.12	1.12	430.20
Females	100	-2 to +2	+0.3 ± 0.07	0.73	236.90

TABLE 38
Measurements (in Millimeters and Grams) in Samples of *Myiarchus panamensis actiosus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	15	93 - 98	95.0 ± 0.41	1.60	1.69
Females	13	87 - 96	92.4 ± 0.72	2.60	2.81
Tail Length					
Males	15	84 - 91	88.3 ± 0.50	1.95	2.21
Females	13	82 - 91	85.9 ± 0.78	2.81	3.27
Body Weight					
Males	0	—	—	—	—
Females	1	—	34.4	—	—
Fourth Primary minus Tenth Primary					
Males	15	+2 to +8	+5.1 ± 0.41	1.58	31.18
Females	13	+4 to +8	+6.1 ± 0.42	1.50	24.65
Fifth Primary minus Ninth Primary					
Males	15	-3 to +1	-0.9 ± 0.27	1.06	122.40
Females	13	-3 to +1	-0.4 ± 0.37	1.33	344.51

uously marked with Antique Brown (except for occasional fringing of external margins). Outer pair of rectrices nearly always with outer vanes scarcely, if at all, paler than inner vanes. Coloration of crown uniform throughout, not noticeably contrasting with that of back. Greater and median upper wing coverts pale-tipped, but not with conspicuous and broad whitish tips as in *M. cephalotes*. Crown and back lighter than in *M. ferox* (closer to Brownish Olive rather than to Fuscous). Tail long, relative to wing; ratio of tail length to

wing length usually 92 percent or more and rarely less than 91 percent. Wing rounded: fifth primary usually equal to or longer than ninth (up to 3 mm. longer) or as much as 1 mm. shorter than ninth, and rarely as much as 2 or 3 mm. shorter than ninth; fourth primary usually at least 5 mm. longer than tenth (up to 11 mm. longer) and rarely less than 4 mm. longer than tenth. Mandible usually all black in fresh specimens, but sometimes slightly paler basally, rarely grayish brown throughout. Color of mouth lining near Spectrum Orange.

Vocal response to intruding conspecifics consists of rasping whistles, hiccups, and an occasional roll, but *no* rasps or "huit" notes. Dawn song consists solely of isolated whistles slowly modulated (vibrato) at frequencies up to 15 Hz.

HABITAT (FIGS. 23, 43, 59): Tropical zone. Open woodlands, brushy pastures, borders of fields, gallery forest, and in mangrove swamps. The species occurs as high as 550 m. in the upper Magdalena valley of Colombia, and has been taken up to 1200 m. in Panama.

BREEDING AND ANNUAL CYCLE: The species is a cavity nester and uses nesting materials similar to other *Myiarchus* species. My only observation of breeding behavior is of a pair investigating a natural cavity at the edge of a mangrove swamp on Isla Puntarenas, Valle, Colombia, on March 26, 1973. This is the same locality where Carol Pearson and Stephen Chaplin (*vide* José Borrero) reported a pair feeding nestlings "in a hole in a large tree at the outer edge of mangroves," in late March 1971. Wetmore (1972) cited the perennial use of a nest box on the side of an isolated, infrequently used building in Panama, and further reported a nest located "in the upper end of a 4-inch [in diameter] metal pipe set at an angle in the ground. The three eggs rested in a soft hollow of opossum fur and balsa down, with a length of shed snakeskin beside them." Burton (1973) has recorded a most unusual nest site for this species, "in a crevice of a low cliff flanking the road on one side," 3 m. above the road. The nest contained the usual fur and shed snakeskin. I know of no other record of ground-nesting in this genus.

The breeding season in most of the range is from late March to early June. February specimens have been taken with the testes measuring only 2 mm. in diameter, whereas a male I took in Panama on April 19 had testes that measured 9 mm. by 5 mm., and another in Colombia had testes that measured 12 mm. by 5 mm. on March 27. A female I collected in Zulia, Venezuela, on May 16 had enlarged ova and an edematous brood patch. W. J. Smith (*in litt.*) observed "an attempted copulation" of a pair on Barro Colorado Island, Panama Canal Zone, as late as May 17. Populations at the higher elevations may breed somewhat later than this,

however. My four specimens from Neiva, at 430 m. in the upper Magdalena valley of Colombia, taken in mid-March, show what I interpret as a light prealternate molt of the body plumage. A fifth specimen, taken at the same locality in late April, appears to be completing this light prealternate molt, which suggests that breeding may occur there from May through July. Juvenals have been taken in Panama as early as June 29, but as late as October 12 at Chicoral, Colombia (upper Magdalena valley, 550 m.).

The complete prebasic molt may commence with some body molt as early as late May in lowland populations. There are specimens showing molt of the remiges from July through September.

VOCAL CHARACTERS: The analysis of vocal characters of *M. panamensis* is based on recordings from these samples:

M. p. panamensis—Panama, three pairs; Colombia, six pairs; Venezuela, three pairs

M. p. actiosus—Costa Rica, three pairs

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 60 and 61.

In response to playback, or when excited by intruding conspecifics, *M. panamensis* vocalizes with repeated hiccups, rasping whistles, and rolls. The hiccup (fig. 60:1-7) is normally a call of two syllables, though occasionally the energy in the two "huit"-like components is continuous. The accent appears to be on the first syllable, probably because the terminal glissando of the second syllable consistently involves the lowest frequencies in the call. Vocally responsive birds deliver long series of these hiccup notes, uninterrupted by other calls. When they do insert another call, it is likely to be a rasping whistle (fig. 60:10-20) with a modulating frequency of 60 to 70 Hz. The carrier frequency in this rasping whistle normally descends slightly, and there is evidence that two sound generators are involved in this call. Highly excited birds may give a series of these rasping whistles, and then render a roll (fig. 61:9-14), a pulsed series of short whistled notes of variable configuration. The introductory component of the roll tends to be of longer duration than those that follow, and the subse-



FIG. 59. Habitat of *Myiarchus panamensis panamensis*. *Top*: Open deciduous woodland in tropical zone near La Jagua, Panama, April 1969; elevation 50 m. Sympatric with *M. tuberculifer brunneiceps* at this locality. *Bottom*: Edge of mangrove and palm plantation on Isla Puntarenas, Bay of Buenaventura, Valle, Colombia, March 1973; elevation sea level.

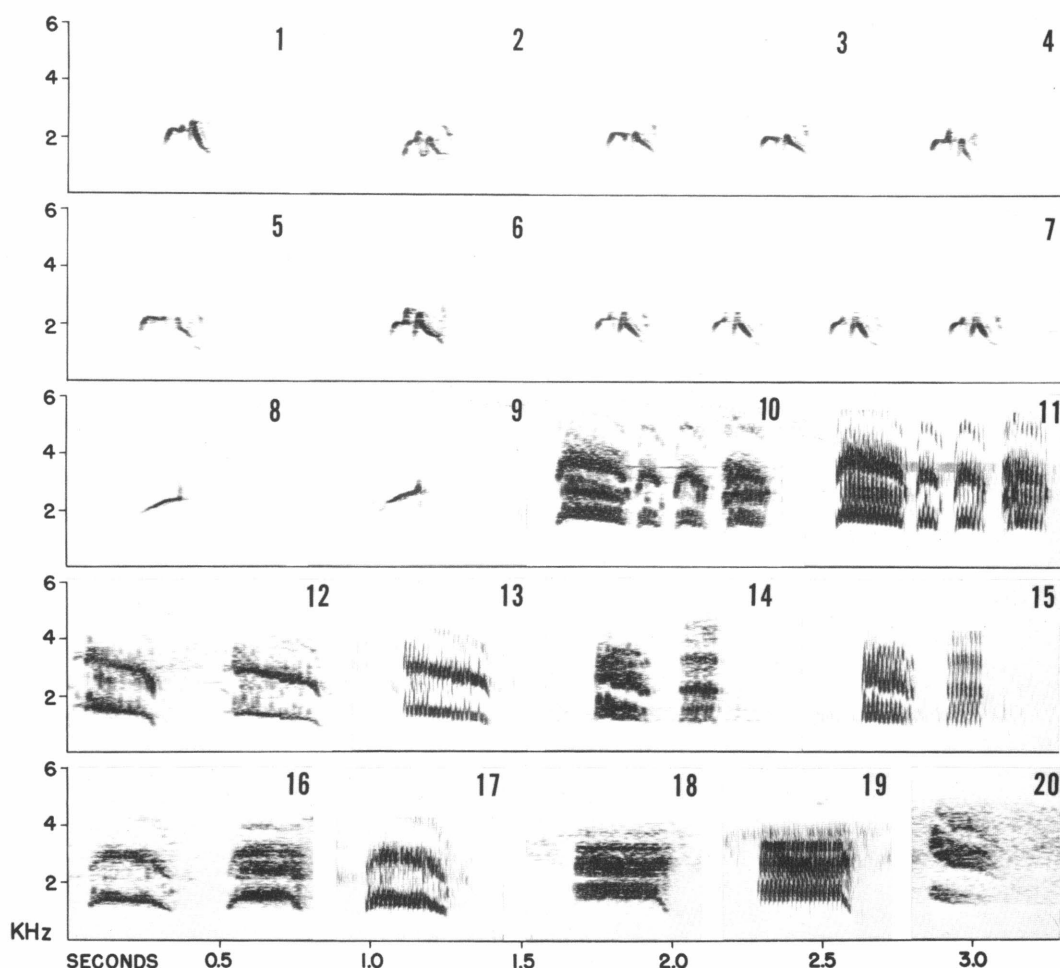


FIG. 60. Variation in vocal characters of *Myiarchus panamensis*: hiccups (1-7), "huit" notes (8, 9), and rasping whistles (10-20). Spectrograms were made from recordings of the following populations: *M. p. actiosus* (Costa Rica, 1, 10, 11); *M. p. panamensis* (Panama, 8, 12, 13; Colombia, 2-5, 9, 14-19; Venezuela, 6, 7, 20). 300 Hz. filter was used for 11, 13, 15, 17, and 19 only.

quent syllables generally decrease slightly in frequency, amplitude, and frequency excursion. Most rolls last for at least 1.5 seconds. There is no evidence that the roll in this species involves two sound generators, as is the case with the rattle of the closely related *M. ferox*. The "huit" call (fig. 60:8, 9), though given occasionally in response to playback, is not a prominent feature of the vocal repertoire of this species.

Foraging birds not excited by playback or

intruding conspecifics deliver short, slowly modulated whistles (vibrato) (fig. 61:1-8) at infrequent intervals. Presumably these calls serve as location notes in the communication between paired birds. These whistled notes are brief, less than 0.3 second in my sample, and are modulated at frequencies up to 15 Hz. Typically, they are single syllables, but they may grade into modified "huit"-like notes or short rolls when the energy becomes pulsed rather than continuous.

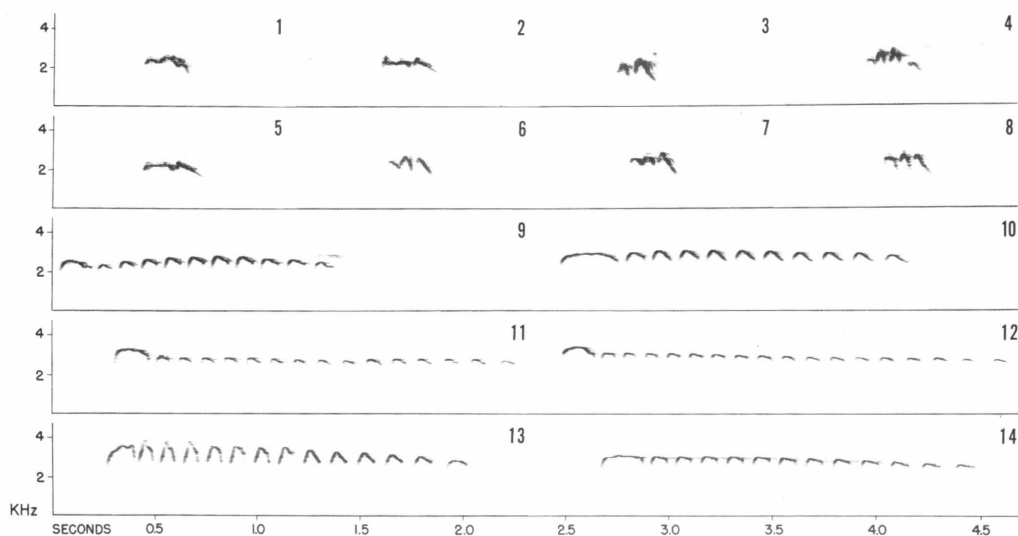


FIG. 61. Variation in vocal characters of *Myiarchus panamensis*: slowly modulated whistles (vibrato) and dawn song (1-8), and rolls (9-14). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. p. actiosus* (Costa Rica, 1, 9); *M. p. panamensis* (Panama, 2-5, 10; Colombia, 6, 7, 11-14; Venezuela, 8).

DAWN SONG: The dawn song of the male *M. panamensis* (fig. 61:1-8) consists of isolated, short, slowly modulated whistles (vibrato) identical with those given by foraging birds during the daylight hours. The only characteristic of the dawn song that sets it apart from the daytime rendition of these calls is the constant frequency with which it is delivered per unit time. The whistled notes in my samples of dawn song were given at intervals of two to three seconds.

GEOGRAPHICAL VARIATION: There is no evidence in my samples to suggest geographical variation in any of the vocal characters of *M. panamensis*.

ITINERARY OF FIELDWORK

- 1969—April 17-21, with *panamensis* at La Jagua, Panamá, Panama.
 1970—May 13-16, with *panamensis* near Carrasquero, Zulia, Venezuela; May 20-21, with *panamensis* near Santa Bárbara, Zulia, Venezuela.
 1973—March 15-19, with *panamensis* near Neiva, Huila, Colombia; March 23, and March 26-27, with *panamensis* on Isla Puntarenas, near Buenaventura, Valle, Colombia.

1974—April 22-24, with *panamensis* near Neiva again.

1976—March 8-9, with *actiosus* near Puntarenas, Puntarenas, Costa Rica.

SYSTEMATICS

Myiarchus panamensis panamensis Lawrence

Myiarchus panamensis Lawrence, 1860, p. 284 (type locality, Atlantic slope of Canal Zone on Panama Railroad; holotype in the American Museum of Natural History, examined). Berlepsch, 1907, p. 477. Morony, Bock and Farrand, 1975, p. 81. Ridgely, 1976, p. 237. Meyer de Schauensee and Phelps, 1978, p. 256.

Myiarchus ferox panamensis: Nelson, 1904, p. 29 (new combination). Ridgway, 1907, p. 640 (synonymy). Oberholser, 1918, p. 306. Todd and Carriger, 1922, p. 346 (synonymy). Todd, 1922, p. 204 (synonymy). Hellmayr, 1927, p. 175 (synonymy). Zimmer, 1938a, p. 15. Meyer de Schauensee, 1950, p. 826. Phelps and Phelps, 1963, p. 189. Slud, 1964, p. 250. Wetmore, 1972, p. 426.

Myiarchus (ferox?) panamensis: Chapman, 1917, p. 475 (synonymy).

Myiarchus ferox audens Wetmore, 1953, p. 5 (type locality, Nuquí, Chocó, Colombia; holotype in

the National Museum of Natural History, examined). Meyer de Schauensee, 1964, p. 278.

DIAGNOSIS: Upper parts browner and abdomen yellowish than in *actiosus*.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 62): Known from the extreme southwestern corner (Pacific coast) of Costa Rica, Panama, the Pacific and Caribbean coasts of Colombia, the lower Cauca and Magdalena valleys and upper Magdalena valley (at least to Neiva) of Colombia, and the Maracaibo region of northwestern Venezuela.

Virtually throughout its range, *M. p. panamensis* is sympatric with the smaller *M. tuberculifer*. In addition, in northern Colombia and northwestern Venezuela it may be sympatric with *M. tyrannulus* and *M. venezuelensis*. In the upper Magdalena valley of Colombia it is sympatric with *M. apicalis*.

I concur with Zimmer (1938a) and Slud (1964) in their interpretation that a single January individual of *panamensis* from El Zapotal, Costa Rica, was a straggler, since this locality is well within the range of *actiosus*.

Specimens examined, 273; localities, by country, from west to east (see fig. 62; asterisks denote author's study areas): COSTA RICA, Rincón de Osa (Puerto Jiménez). PANAMA, Boquerón, Chiriquí (Puerto Armuelles; El Volcán; Boquete); Almirante, Bocas del Toro; Las Lajas, Chiriquí (Isla Parida; Isla Brava); Isla de Coiba (Islas Contreras; Isla Afuerita; Isla Ranchería); Soná, Veraguas; Santa Fé, Veraguas; Santiago, Veraguas (El Villano; Aguadulce, Coclé; El Rincón, Parita, and Monagrillo, in Herrera); El Coco, Coclé (El Valle; El Potrero; El Uracillo); Isla Iguana, Los Santos (Tonosí; Pedasí); Nueva Gorgona, Panamá (Bejuco; La Campana); *La Jagua, Panamá (Canal Zone; Pacora; La Chorrera; Ft. San Lorenzo; Isla Taboga; Isla Taboquilla; Isla Uravá; Archipelago de las Perlas; Mandinga, Colón; Chimán, Panamá; Jaqué, Darién. COLOMBIA, Tumaco, Nariño; *Buenaventura, Valle (Bahía de Málaga); Nuquí, Chocó; Sautatá, Chocó; Nicoclí, Antioquia; Villa Artiaga, Antioquia; Quimarí, Córdoba (Río Sinú); Bagadó, Chocó; Lorica, Bolívar; Turbaco, Bolívar; Colosó, Sucre; *Neiva, Huila; Calamar, Bolívar; Chicoral, Tolima; Santa Marta, Magdalena (Bonda; Buritaca); Gamarra, Mag-

dalena (La Gloria; Aguachica; Río Viejo, and Regeneración, Bolívar); Simití, Bolívar; Puerto Berrio, Antioquia (Malena); Casacará, Cesar; La Raya, Cesar; El Tambor, Santander. VENEZUELA, *Carrasquero, Zulia (Río Guasare); *Santa Bárbara, Zulia (Encontrados); El Vigía, Mérida; Mene Grande, Zulia.

REMARKS: Until the release of information acquired in my study (Morony, Bock and Farand, 1975; Ridgely, 1976; Meyer de Schauensee and Phelps, 1978), *panamensis* had been considered by all recent workers to be a representative subspecies of *M. ferox*, with *venezuelensis* being regarded as the intermediate form, both geographically and morphologically. I have discussed elsewhere (p. 496) the rela-

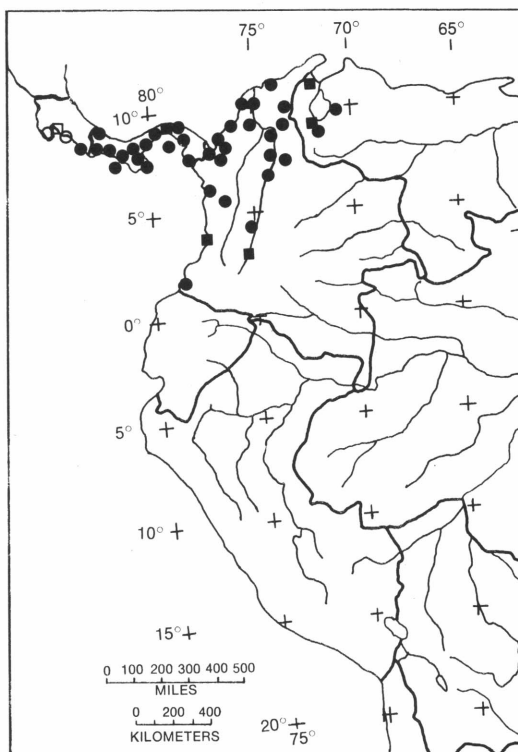


FIG. 62. Distribution of *Myiarchus panamensis* (solid circles and squares) and of *M. p. actiosus* (open circles and square) as indicated by localities of specimens examined (circles) and by sites where author studied the species in the field (square). See pages 561 and 563 for lists of these localities and page 560 for an itinerary of author's fieldwork with this species.

tionship of *M. panamensis* with *M. ferox* and *M. venezuelensis* and the evidence for sympatry of *M. panamensis* and *M. venezuelensis* in northern Colombia and northwestern Venezuela. Because of this sympatry and the fact that their vocal characters are very different, it was not necessary for me to use experimental playback to clarify the relationships of these two forms. Vocally, *M. panamensis* is closest to *M. ferox*, a completely allopatric species found east of the Andes. Although there are prominent differences between the vocal repertoires of these two species, well exceeding the usual differences between the voices of sympatric species of *Myiarchus*, I was curious to see what, if any, response I might get from territorial *panamensis* to the experimental playback of a *M. ferox* tape. I found that the reconnaissance tape made from the voice of *M. ferox* was of no value in locating pairs of *M. panamensis*, and the reverse was equally true. On the island of Puntarenas, Valle, Colombia, I conducted the following series of playback experiments, on March 26, 1973; they illustrate the ability of a pair of *M. panamensis* to discriminate between its own vocal repertoire and that of *M. ferox*:

Experiment 10—study area two. Tapes used, *M. ferox* vs. *M. phaeocephalus*. Birds silent, location unknown at start at 5:03 P.M. No show at all during the first half; cable switch at 5:10. No response during second half. One bird appeared, silent, at 5:16, about 5 ft. from *phaeocephalus* model, then moved out to 25 ft. (back into the mangroves) by the end of the experiment.

Experiment 11—same locality, pair, and date as above. Tapes used, *M. ferox* vs. *M. panamensis*. Birds still presumably in the general area, but silent and exact location unknown. Start at 5:24 P.M. Within 30 seconds, two birds appeared within *panamensis* area, giving hiccups and rolls. Crisscross of *panamensis* at 5:25. Another good roll. Both still in *panamensis* area at 5:27. Another crisscross of *panamensis* area at 5:28, and a good roll. A pass at *panamensis* model at 5:29. One bird perched 2 ft. from *panamensis* speaker, the other perched 15 ft. from *panamensis* model. Crisscross at 5:29:30. One moved over to within 30 ft. of *ferox* model briefly, then flew back to *panamensis* area, 10 ft. from that model. Good roll, just 10 ft. from *panamensis*

model. Crisscross, 15 ft. from model at 5:31. Another crisscross, and both birds 35 ft. from *panamensis* model. At that position at cable switch at 5:31. Both reoriented to new *panamensis* area within 20 seconds. Both 15 ft. above new *panamensis* model. One moved to 5 ft. of model at 5:33. Crisscross of new area. Both birds moved back to *ferox* area briefly, where they gave some rolls, but then returned to within 25 ft. of *panamensis* model. Crisscross of *panamensis* model. Back to midpoint, at 5:35, then by 5:36 both were back within 40 ft. of *panamensis* model. One moved in to 15 ft. of *panamensis* model, giving hiccups and rolls. Both birds 25 ft. from model. Another crisscross, then out to 30 ft. One to midpoint. But both birds within 30 ft. of *panamensis* model at end of experiment.

Experiment 12—same locality, pair, and date as above. Tapes used, *M. venezuelensis* vs. *M. tuberculifer*. Birds silent, location unknown. Start at 5:45 P.M. One gave a hiccup over *tuberculifer* model, 30 ft. up, at 5:48, then flew back into mangroves. No further response, and discontinued experiment at cable switch.

Experiment 13—same locality, pair, and date as above. Tapes used, *M. ferox* vs. *M. venezuelensis*. Birds silent, location unknown at start at 5:55 P.M. Within 20 seconds, one bird gave a single roll from outside the experimental area. Two birds appeared at edge of area at 5:57, giving hiccup notes. One moved to within 15 ft. of *ferox* model very briefly. Then birds became quiet, location unknown. No further response up to cable switch at 6:02. Discontinued this experiment at that point.

Experiment 14—same locality, pair, and date as above. Tapes used, *M. panamensis* vs. *M. tuberculifer*. Birds still silent, location unknown at start at 6:04 P.M. Within 30 seconds, a bird gave a roll. Crisscross of *panamensis* model at 6:05. In a study at 6 ft. from *panamensis* model. Crisscross. Another crisscross. Gave rolls about 2 ft. from model, then dropped down to vicinity of the *panamensis* speaker. More rolls. Both birds giving hiccup notes within 10 ft. of *panamensis* model. In a study at 2 ft. Cable switch at 6:11. Birds moved out to midpoint within 30 seconds. Both moved over to new *panamensis* area by 6:12:30. To within 2 ft. of *panamensis* model by 6:13. Had to discontinue experiment prematurely because the tide is coming in from the mangroves. This has been an interesting series of experiments, demonstrating clearly an ability to discriminate between *M. panamensis*, *M. ferox*, and *M. venezuelensis*.

TABLE 39
Measurements (in Millimeters) in Combined Samples of Both Subspecies of *Myiarchus panamensis*

Measurement	N	Range	Mean, S.E.	S.D.	C.V.
Ratio of Tail Length to Wing Length	204	90 - 100	94.9 $\pm$ 0.15	2.11	2.23
Fifth Primary minus Ninth Primary	209	-3 to +3	+0.2 $\pm$ 0.07	1.01	621.28
Fourth Primary minus Tenth Primary	214	+2 to +11	+6.9 $\pm$ 0.11	1.68	24.32

The lower mandibles in my small series of specimens from Neiva in the upper Magdalena valley of Colombia are noticeably paler (less black) than in those specimens I have taken elsewhere in Colombia, Panama, and Venezuela, but I can see no other consistent morphological differences. I have already alluded to the probability that the birds in the upper Magdalena valley breed somewhat later than the species does elsewhere, but this could be a function of altitude and a subtle effect on the habitat. In any event, in the absence of other demonstrable differences, I would prefer not to recognize this population formally. Similarly the characters of Wetmore's *audens* (1953) along the Pacific coast of Colombia are not well enough developed, in my opinion, to warrant formal recognition.

Myiarchus panamensis actiosus Ridgway

Myiarchus ferox actiosus Ridgway, 1906, p. 116 (type locality, Pigres, Gulf of Nicoya, Costa Rica; holotype in the National Museum of Natural History, examined). Ridgway, 1907, p. 640 (synonymy). Carriker, 1910, p. 694. Oberholser, 1918, p. 306. Hellmayr, 1927, p. 175 (synonymy). Zimmer, 1938a, p. 15. Slud, 1964, p. 250.

DIAGNOSIS: Upperparts decidedly grayer and abdomen paler (less yellow) than in *panamensis*.

MYIARCHUS FEROX (GMELIN)

This widespread but endemic South American species is found virtually throughout the tropical zone of northern and central South America, east of the Andes and south to extreme northeastern Argentina and southeastern Brazil (fig. 70). The species has heretofore included such forms as *venezuelensis*, "in-

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 62): Known only from the Pacific coast of Costa Rica, where found principally in mangroves, from the shores of the Gulf of Nicoya southward to some point north of the Osa Peninsula.

I found *actiosus* to be sympatric with *M. tuberculifer* in the mangroves near Puntarenas, and at one point could hear *M. tyrannulus* at the edge of the mangroves. For the most part, however, *actiosus* must be parapatric with *M. tyrannulus* and *M. nuttingi* (a widespread Middle American species), since these two species prefer more xeric habitat.

Specimens examined, 28; localities, from west to east (see fig. 62; asterisk denotes author's study area): COSTA RICA, Punta Piedra, Puntarenas; *Puntarenas, Puntarenas (El Zapotal; Barranca; Pigres; Isla San Lucas); Parrita, Puntarenas.

REMARKS: When I visited Puntarenas in March 1976 I had no difficulty in locating pairs of *actiosus* with which to work, using a reconnaissance tape made from recordings of Colombian *panamensis*. The resident birds in the mangrove swamps near Puntarenas were very responsive to the vocal characters of the Colombian birds, and a subsequent spectrographic comparison of the vocal repertoires of the two subspecies revealed no differences (p. 560).

sulicola," *panamensis*," *audens*," and *actiosus*, but data collected in this study indicate that these forms do not belong with *M. ferox*. The species is polytypic, however, with three subspecies (*brunnescens*, *ferox*, and *australis*) recognized here, and is nonmigratory.

DIAGNOSIS: One of the larger (see measure-

ments in tables 40 and 41) "dark-tailed" species, i.e., rectrices of adults not conspicuously marked with Antique Brown (other than fringing

in fresh plumage in some populations). Outer vane of outer rectrix only barely if at all paler than inner vane. Coloration of crown uni-

TABLE 40
Wing Length (in Millimeters) in Samples of *Myiarchus ferox*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. f. ferox</i>					
Males	117	80 - 93	88.6 ± 0.19	2.07	2.34
Females	96	81 - 91	85.8 ± 0.23	2.29	2.67
Intergrades between <i>ferox</i> and <i>brunnescens</i>					
Males	59	85 - 93	88.8 ± 0.29	2.24	2.52
Females	46	83 - 94	86.2 ± 0.35	2.34	2.72
<i>M. f. brunnescens</i>					
Males	21	84 - 92	89.0 ± 0.44	2.04	2.29
Females	18	82 - 90	85.8 ± 0.46	1.96	2.28
Intergrades between <i>ferox</i> and <i>australis</i>					
Males	32	85 - 91	88.4 ± 0.33	1.88	2.13
Females	27	82 - 88	84.4 ± 0.39	2.01	2.38
<i>M. f. australis</i>					
Males	111	83 - 95	89.8 ± 0.22	2.35	2.61
Females	105	81 - 93	86.1 ± 0.24	2.46	2.85
Combined Samples of All Subspecies					
Males	340	80 - 95	89.1 ± 0.12	2.24	2.51
Females	292	81 - 94	85.8 ± 0.14	2.35	2.74

TABLE 41
Tail Length (in Millimeters) in Samples of *Myiarchus ferox*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. f. ferox</i>					
Males	119	79 - 93	86.6 ± 0.27	2.92	3.37
Females	98	76 - 90	83.5 ± 0.28	2.79	3.34
Intergrades between <i>ferox</i> and <i>brunnescens</i>					
Males	58	79 - 94	85.7 ± 0.42	3.16	3.69
Females	46	78 - 92	83.0 ± 0.41	2.78	3.36
<i>M. f. brunnescens</i>					
Males	22	80 - 91	85.8 ± 0.61	2.84	3.32
Females	17	79 - 85	81.9 ± 0.47	1.92	2.34
Intergrades between <i>ferox</i> and <i>australis</i>					
Males	34	78 - 91	86.2 ± 0.51	2.99	3.47
Females	27	78 - 87	82.3 ± 0.47	2.43	2.96
<i>M. f. australis</i>					
Males	111	81 - 94	88.1 ± 0.28	2.94	3.33
Females	108	77 - 91	83.8 ± 0.31	3.23	3.86
Combined Samples of All Subspecies					
Males	344	78 - 94	86.8 ± 0.17	3.09	3.56
Females	296	76 - 92	83.3 ± 0.17	2.93	3.51

form throughout and not noticeably contrasting with that of back. Crown and back darker than in *M. panamensis* (closer to Fuscous rather than to Brownish Olive). Tail long, relative to wing; ratio of tail length to wing length usually 94 percent or more and rarely less than 93 percent. Wing rounded: fifth primary usually equal to or longer than ninth (up to 5 mm. longer) and rarely more than 1 mm. shorter than ninth; fourth primary usually at least 5 mm. longer than tenth (up to 12 mm. longer) and rarely less than 4 mm. longer than tenth. In fresh specimens, entire mandible black, with no seasonal or geographical variation, but paling occurs with age, rendering this character unreliable in older specimens (fig. 21). Color of mouth lining near Spectrum Orange.

Vocal responses to intruding conspecifics consist of rasping whistles, hiccups, and an occasional strident rattle, but *no* rolls, rasps, or "huit" notes. Dawn song consists solely of isolated whistled notes slowly modulated (vibrato) at frequencies of 15 to 30 Hz.

HABITAT (FIGS. 22, 27-29, 63, 64, 78): Tropical zone. Clearings in forested areas, bor-

ders of woodlands, wooded areas along rivers and streams, disturbed agricultural areas (e.g., coffee and cocoa plantations), wooded savannas; habitats tend to be more mesic than arid. The species has been taken up to 425 m. in Tachira, Venezuela; up to 1375 m. in Cuzco, Peru; up to 920 m. in Rio de Janeiro, Brazil.

BREEDING AND ANNUAL CYCLE: The species is a cavity nester and uses materials similar to those of other members of the genus. In December 1970 François Haverschmidt showed me a cavity in a low tree (*Curatella americana*) on the Hannover savanna near Zanderij, Surinam; the cavity had been used in the past by *M. ferox*. He has noted (Haverschmidt, 1968) that the species "nests in holes in trees; the hole is lined with snake skins." Werner Bokermann sent me a photograph (fig. 65) of a natural cavity used as a nest site along the Rio Liberdade, Mato Grosso, Brazil. The cavity was 90 cm. above the ground and lined with feathers, shed skin of snakes and lizards, and vegetable fibers. There were two eggs in this nest on August 10, 1975; a photograph of one of the eggs suggests markings similar to those

TABLE 42
Ratio of Tail Length to Wing Length (in Percentage) in Samples of *Myiarchus ferox*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. f. ferox</i>					
Males	111	92 - 102	97.8 ± 0.20	2.13	2.18
Females	95	92 - 102	97.5 ± 0.22	2.13	2.19
Intergrades between <i>ferox</i> and <i>brunnescens</i>					
Males	56	92 - 102	96.6 ± 0.32	2.39	2.48
Females	45	92 - 101	96.4 ± 0.35	2.36	2.45
<i>M. f. brunnescens</i>					
Males	21	93 - 99	96.4 ± 0.52	2.38	2.47
Females	17	92 - 98	95.5 ± 0.45	1.84	1.93
Intergrades between <i>ferox</i> and <i>australis</i>					
Males	31	92 - 101	97.7 ± 0.40	2.25	2.30
Females	26	94 - 100	97.3 ± 0.35	1.76	1.81
<i>M. f. australis</i>					
Males	110	93 - 104	98.3 ± 0.18	1.93	1.96
Females	106	92 - 104	97.3 ± 0.23	2.39	2.45
All Subspecies of <i>M. ferox</i>					
Males	329	92 - 104	97.7 ± 0.12	2.22	2.28
Females	289	92 - 104	97.1 ± 0.13	2.27	2.34
Both sexes	618	92 - 104	97.4 ± 0.09	2.26	2.32

TABLE 43
Fifth Primary minus Ninth Primary (in Millimeters) in Samples of *Myiarchus ferox*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. f. ferox</i>					
Males	90	-1 to +3	+1.0 ± 0.09	0.86	84.24
Females	74	-1 to +5	+1.1 ± 0.13	1.08	97.46
Intergrades between <i>ferox</i> and <i>brunnescens</i>					
Males	44	-1 to +4	+1.3 ± 0.17	1.12	89.86
Females	34	-1 to +4	+1.5 ± 0.21	1.21	80.82
<i>M. f. brunnescens</i>					
Males	16	-1 to +2	+0.8 ± 0.25	1.00	133.33
Females	15	0 to +3	+1.1 ± 0.23	0.88	82.85
Intergrades between <i>ferox</i> and <i>australis</i>					
Males	24	-1 to +3	+0.8 ± 0.17	0.82	98.02
Females	22	-1 to +3	+0.9 ± 0.19	0.89	102.92
<i>M. f. australis</i>					
Males	38	-1 to +3	+1.2 ± 0.18	1.09	91.78
Females	33	0 to +3	+1.2 ± 0.18	1.04	88.38
All Subspecies of <i>M. ferox</i>					
Males	212	-1 to +4	+1.1 ± 0.07	0.97	91.98
Females	178	-1 to +5	+1.2 ± 0.08	1.07	91.93
Both sexes	390	-1 to +5	+1.1 ± 0.05	1.02	92.06

TABLE 44
Fourth Primary minus Tenth Primary (in Millimeters) in Samples of *Myiarchus ferox*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. f. ferox</i>					
Males	107	+4 to +11	+7.7 ± 0.15	1.57	20.39
Females	87	+4 to +12	+8.0 ± 0.17	1.61	20.16
Intergrades between <i>ferox</i> and <i>brunnescens</i>					
Males	50	+5 to +11	+7.7 ± 0.24	1.73	22.45
Females	39	+5 to +11	+7.9 ± 0.29	1.83	23.05
<i>M. f. brunnescens</i>					
Males	19	+4 to +10	+7.2 ± 0.41	1.80	25.19
Females	16	+4 to +10	+7.0 ± 0.37	1.46	20.87
Intergrades between <i>ferox</i> and <i>australis</i>					
Males	31	+6 to +11	+7.9 ± 0.25	1.36	17.20
Females	26	+6 to +10	+7.8 ± 0.19	0.98	12.56
<i>M. f. australis</i>					
Males	105	+3 to +11	+7.3 ± 0.15	1.59	21.76
Females	101	+3 to +11	+7.2 ± 0.17	1.73	24.08
All Subspecies of <i>M. ferox</i>					
Males	312	+3 to +11	+7.5 ± 0.09	1.61	21.26
Females	269	+3 to +12	+7.6 ± 0.10	1.67	21.96
Both sexes	581	+3 to +12	+7.6 ± 0.07	1.63	21.58

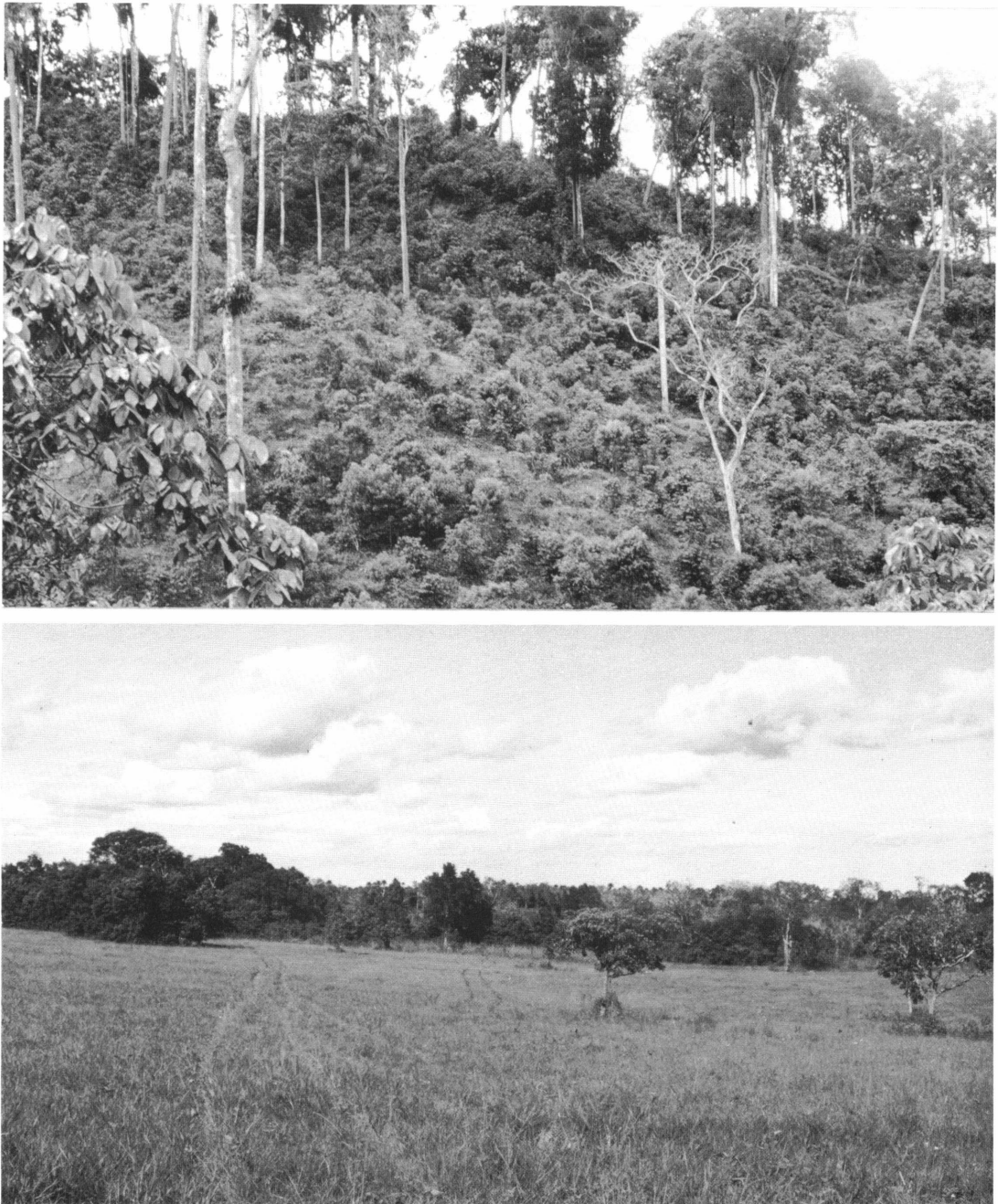


FIG. 63. *Top*: Habitat of *Myiarchus ferox ferox* in a coffee plantation near Tingo María, Huánuco, Peru, November 1972; elevation 800 m. *Bottom*: Habitat of *M. ferox* (intergrades between *ferox* and *brunnescens*) in open woodland in tropical zone near Lago Mozambique, Puerto Lopez, Meta, Colombia, May 1970; elevation 400 m. Sympatric with *M. t. tuberculifer* at this locality.

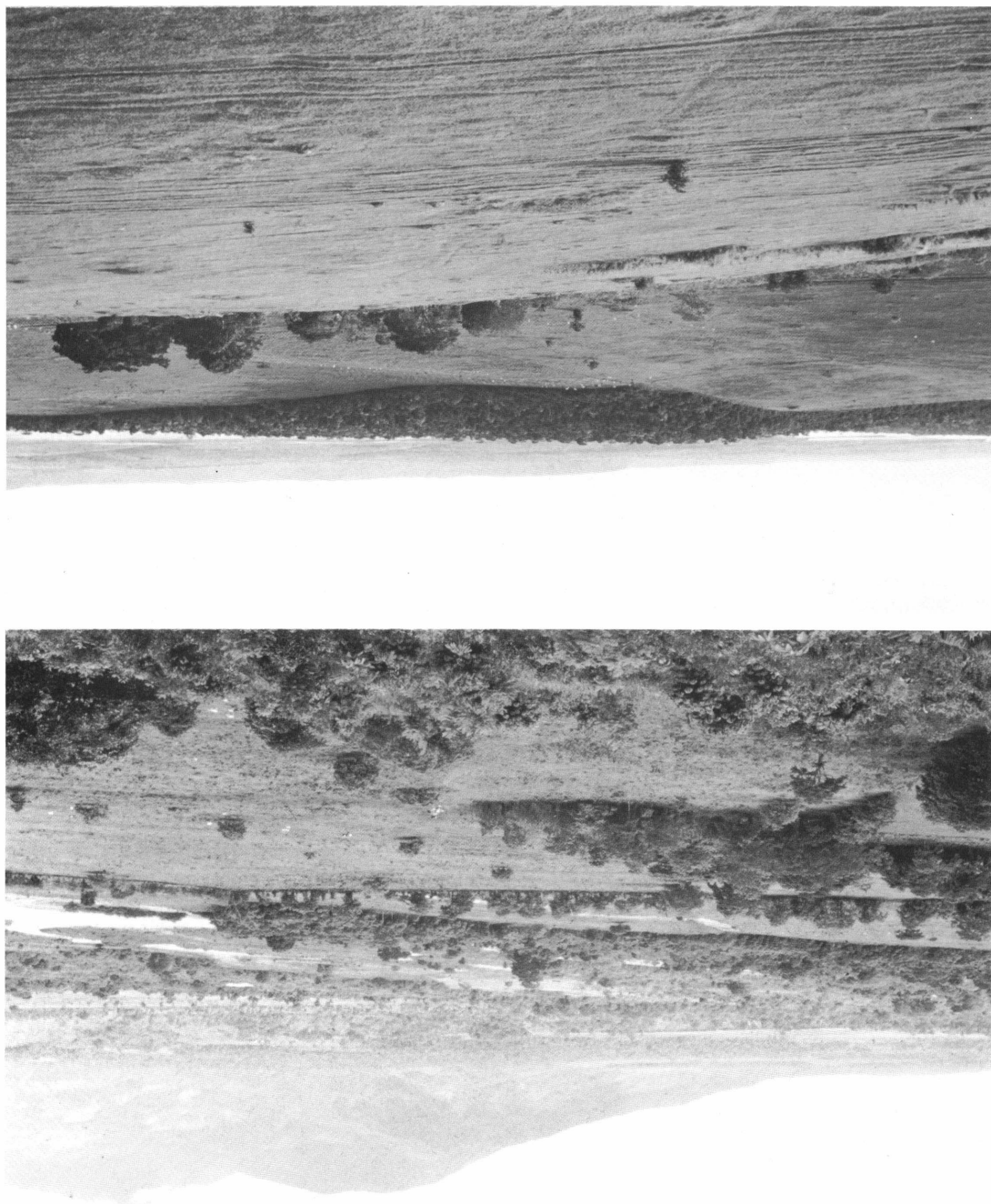


FIG. 64. *Top*: Habitat of *Myiarchus ferox brunneus* in open woodland (llanos) along the Río Uribante, Táchira, Venezuela, May 1969; elevation 400 m. *Bottom*: Habitat of *M. f. australis* in patches of woodland on the Fazenda Barreiro Rico, near Anhembi, São Paulo, Brazil, December 1970; elevation 500 m. Sympatric with *M. s. swainsoni* and *M. tyrannulus bahiae* at this locality.

TABLE 45
Body Weight (in Grams) of Combined Samples of All Subspecies of *Myiarchus ferox*

Sex	N	Range	Mean, S.E.	S.D.	C.V.
Males	33	21.0 - 33.0	26.98 ± 0.40	2.31	8.58
Females	43	23.5 - 34.0	27.84 ± 0.34	2.20	7.92



FIG. 65. Natural cavity used as a nest site by *Myiarchus f. ferox* in Mato Grosso, Brazil. There were two eggs in the nest on August 10, 1975. Photograph courtesy of Werner Bokermann.

of *M. crinitus*. One of the birds in attendance was collected, and I was able to confirm the identification as *M. ferox*.

The breeding season for the two southern subspecies, *ferox* and *australis*, is not synchronized and breeding may occur from July into December. A large series taken near Iquitos, Peru (FMNH) includes June specimens marked "testes not enlarged" and July specimens marked "testes slightly enlarged." A specimen (USNM 516466) taken in Pará, Brazil, on July 23 had testes that measured 12 mm.

by 6 mm. Many specimens collected from August through November have been in breeding condition. The testes of three males I collected in late November in Argentina varied in size from 9 to 10 mm. by 6 mm. A female taken at the same time had the oviduct enlarged, ova up to 2 mm. in diameter and the abdomen becoming edematous. On November 21 I collected a male in southeastern Peru in which the testes measured only 4 by 3 mm., indicating a post-breeding condition. Juvenal-plumaged specimens of the two southern subspecies are known from September through April.

The Venezuelan subspecies *brunnescens*, and most of the populations intermediate between *ferox* and *brunnescens*, found north of the equator, breed from March through May. Testes of eight males I collected in May varied in size from 9 to 11 mm. by 4 to 6 mm., whereas October specimens had testes averaging 4 by 2 mm. A female taken on May 24 had the oviduct enlarged, ova up to 1.5 mm., and the abdomen slightly edematous. The breeding of *brunnescens*, then, is completely out of phase with that of nominate *ferox* and of *australis*; *brunnescens* is actively breeding at a time when *ferox* and *australis* are in fresh plumage or are just completing the annual molt.

A lack of synchrony in the timing of the prebasic molt in nominate *ferox* is presumably correlated with differences in the timing of breeding, which may in turn be due to differences in the timing of the rainy season from one year to the next. The majority of specimens of *ferox* show active molt of the remiges and rectrices from late November through early June. The more southern *australis* has a similar molt schedule, though possibly with greater synchronization, for most specimens showing molt of the flight feathers have been taken from December through May. Specimens of the northern *brunnescens* taken in April and May are in worn to very worn plumage, whereas

specimens taken in October and November are in fresh plumage. Three of the 12 very worn specimens I collected in late May had already begun their body molt. These data indicate that the molt schedule of *brunnescens* is completely out of phase with that of nominate *ferox*, for *brunnescens* is in fresh plumage at a time when *ferox* is in very worn plumage or just commencing its annual molt.

Juvenals acquire their definitive plumage by a complete molt at approximately the same time as that of the adults. Juvenals of nominate *ferox* and *australis*, showing active postjuvinal molt, are known from January through July.

VOCAL CHARACTERS: The analysis of vocal characters of *M. ferox* is based on recordings from these samples:

M. f. ferox—Surinam, two pairs; Peru, three pairs

M. f. brunnescens—Venezuela, four pairs

M. f. australis—Argentina, three pairs; Brazil, seven pairs

Intergrades between *M. f. ferox* and *M. f. brunnescens*—Venezuela, seven pairs; Colombia, two pairs

Intergrades between *M. f. ferox* and *M. f. australis*—Brazil, one pair; Bolivia, two pairs

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 66 to 69.

In response to playback, or when excited by intruding conspecifics, *M. ferox* vocalizes with repeated hiccups, rasping whistles, and rattles. The hiccup (fig. 66:16-26) is normally a call of two syllables, though occasionally the energy in the two "huit"-like components is continuous. The accent appears to be on the first syllable by virtue of its greater amplitude and longer duration. Hiccups often are given in a rapid sequence by a highly motivated bird, but may be rendered in a random fashion with rasping whistles and rattles. In the rasping whistle (fig. 67:1-12) the carrier frequency is modulated at a frequency of 40 to 50 Hz. and descends very gradually. There is evidence that, as in the closely related *M. panamensis*, two sound generators are involved in the production of this call. The most diagnostic call used by *M. ferox* in response to playback is the rattle (figs. 68,

69), which is unique in the genus. This is a prolonged call, from 1.0 to 4.0 seconds long in my samples, characterized by a very penetrating and strident quality. Unlike the homologous roll of its congeners, including that of the closely related *M. panamensis*, the rattle is frequently and perhaps invariably produced from two sound generators. The two sound sources are producing basically the same signal, but their relationship to each other often is a discordant one, and hence the strident quality. This dissonant relationship of the two resulting signals can be demonstrated spectrographically with a display made at half normal speed, as in figure 69:6. Less often, vocal response to playback may include "huit" notes (fig. 66:27-31) and a series of relatively short, high-pitched whistles (fig. 67:13-20). These calls are not prominent in the repertoire of this species, however.

Foraging birds not excited by playback or intruding conspecifics deliver short, slowly modulated whistles (vibrato) (fig. 66:1-15) at infrequent intervals. Presumably these calls serve as location notes in the communication between paired birds. I have elicited this call from a bird whose mate had recently been removed by collecting. Normally, these whistled calls are brief, averaging from 0.2 to 0.3 second in my samples, but they may last as long as 1.2 seconds. The modulating frequency is from 15 to 30 Hz. Each of these calls begins as a short, whistled note, but some become pulsed into modified "huit" notes or a short roll; this emphasizes the gradation between these basic types of calls.

DAWN SONG: The dawn song of male *M. ferox* (fig. 66:1-15) consists of isolated, short, slowly modulated whistles (vibrato) identical with those given by foraging birds during daylight hours. The only characteristic of the dawn song that sets it apart from the daytime rendition of these calls is the constant frequency with which it is delivered per unit time. In my samples of dawn song the whistled notes were given at intervals of three to four seconds.

GEOGRAPHICAL VARIATION: There is no evidence in my samples to suggest that there is geographical variation in any of the vocal characters of *M. ferox*.

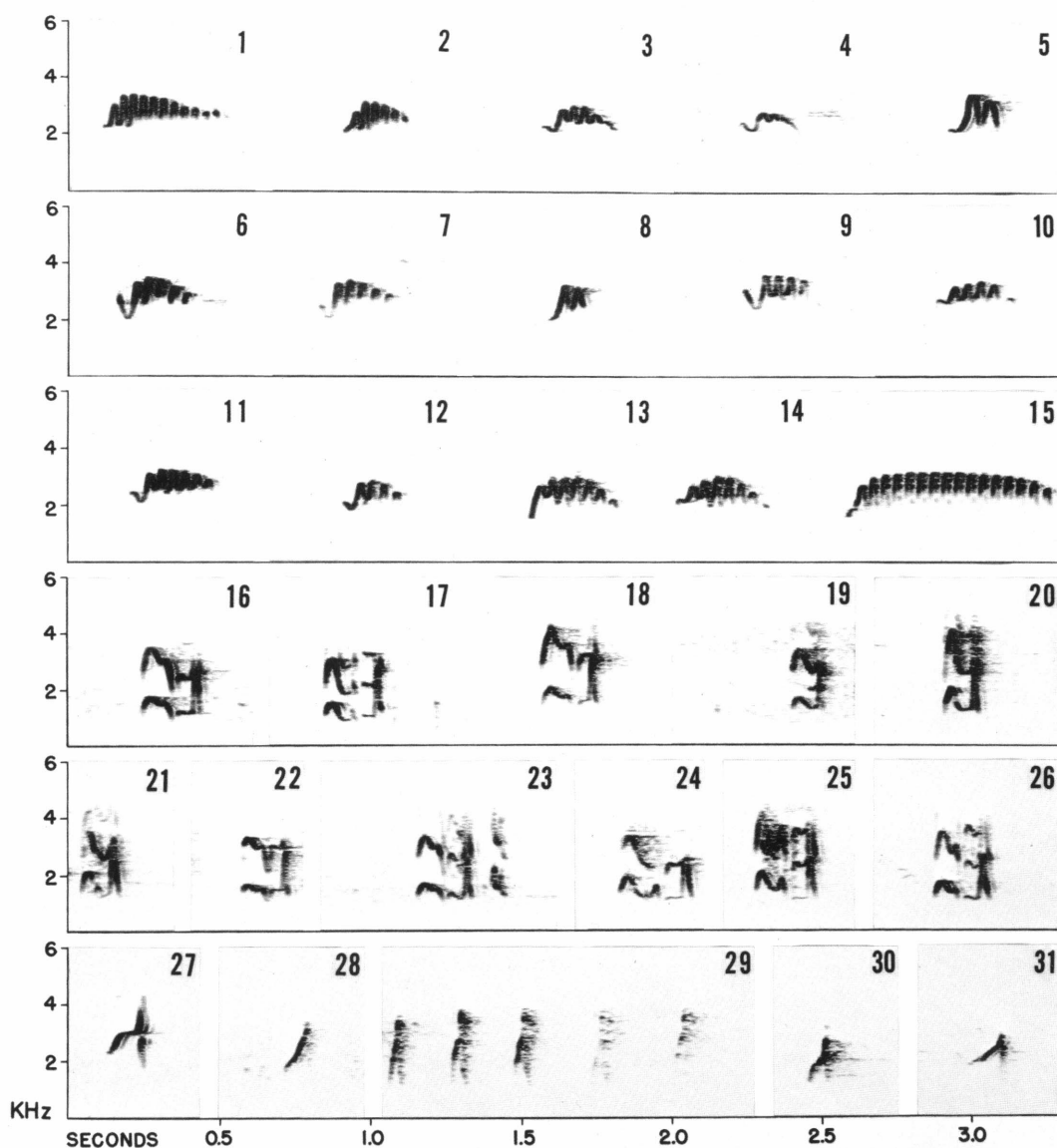


FIG. 66. Variation in vocal characters of *Myiarchus ferox*: slowly modulated whistles (vibrato) and dawn song (1-15), hiccups (16-26), and "huit" notes (27-31). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. f. ferox* (Surinam, 1, 2, 17, 27; Peru, 3, 4, 16, 28, 29); *M. f. brunescens* (Venezuela, 19, 20); *M. f. australis* (Argentina, 12, 26; Brazil, 13-15, 24, 25, 31); intergrades between *M. f. ferox* and *M. f. brunescens* (Colombia, 5, 21, 22; Venezuela, 6-8, 18); intergrades between *M. f. ferox* and *M. f. australis* (Bolivia, 9, 10, 23, 30; Brazil, 11).

ITINERARY OF FIELDWORK

1967—December 12, with intergrades between *ferox* and *australis* near Ipatinga, Minas Gerais, Brazil.

1969—May 12-16, with *brunescens* near San Fernando de Apure, Apure, Venezuela (and neighboring Guárico); May 20-23, with *brunescens* near Barinas, Barinas, Venezuela;

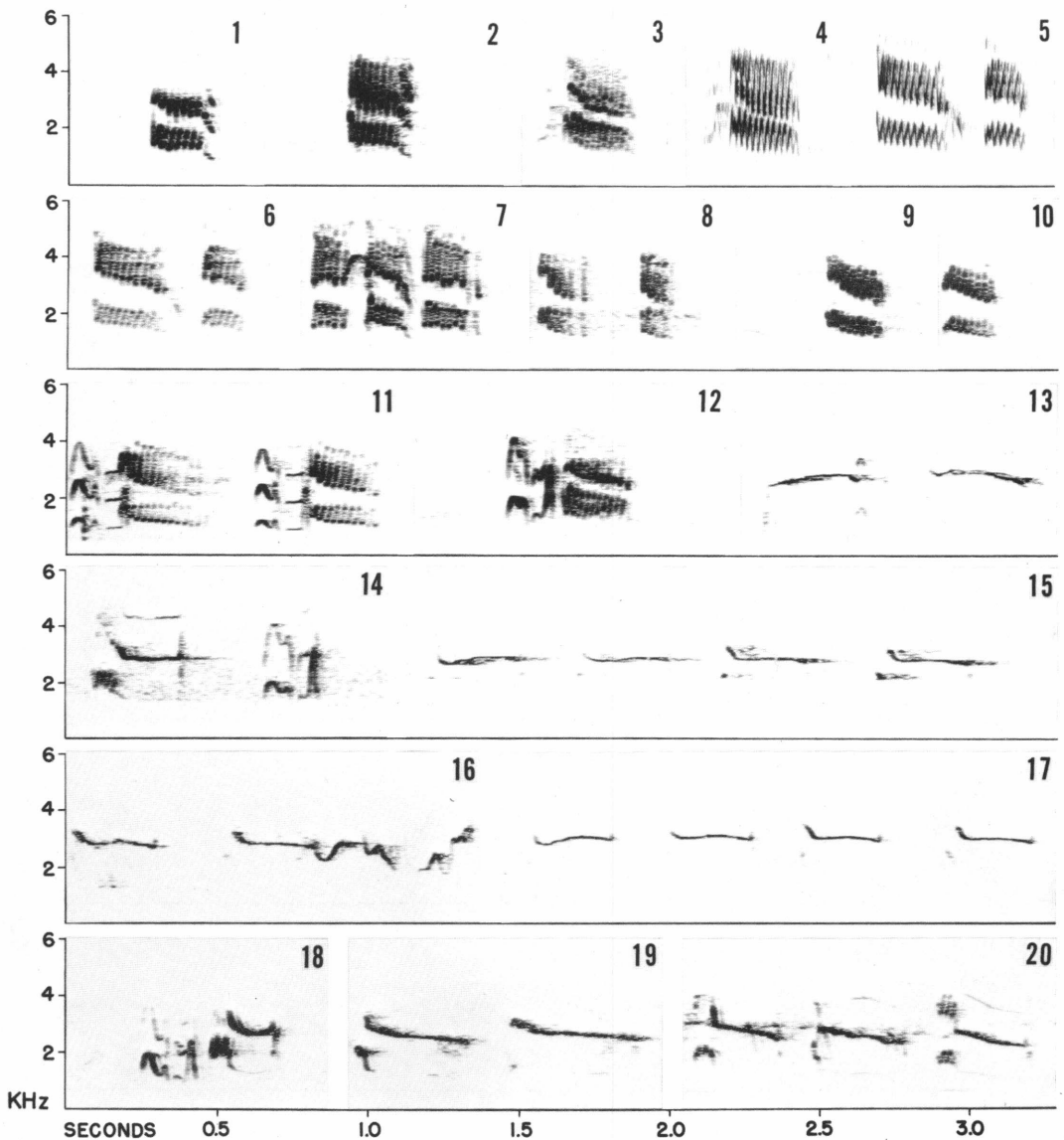


FIG. 67. Variation in vocal characters of *Myiarchus ferox*: rasping whistles (1-12) and series of whistles (13-20). Spectrograms were made from recordings of the following populations: *M. f. ferox* (Surinam, 1, 2, 11, 13; Peru, 3, 4, 12); *M. f. brunescens* (Venezuela, 7, 16, 17); *M. f. australis* (Brazil, 9, 19; Argentina, 10, 20); intergrades between *M. f. ferox* and *M. f. brunescens* (Venezuela, 5, 6, 14; Colombia, 15); intergrades between *M. f. ferox* and *M. f. australis* (Bolivia, 8, 18). 300 Hz. filter was used for 4 and 5 only.

May 23-26, with *brunescens* near the Río Chururu and Santo Domingo, Táchira, Venezuela.

1970—April 30 through May 9, with intergrades between *ferox* and *brunescens* in north-

eastern Bolívar, Venezuela (El Callao, Tumeremo, El Palmar, and El Manteco) and near La Morrocuya, Monagas, Venezuela; May 7, with intergrades between *ferox* and *brunescens* near Maripa, Bolívar, Venezuela;

May 25-27, with intergrades between *ferox* and *brunnescens* near Villavicencio, Meta, Colombia; November 14-22, with *australis* at Las Tres Marías, Corrientes, Argentina; De-

cember 9-14, with *australis* at Fazenda Barreiro Rico, near Anhembi, São Paulo, Brazil; December 16-22, with *ferox* near Zanderij, Surinam.

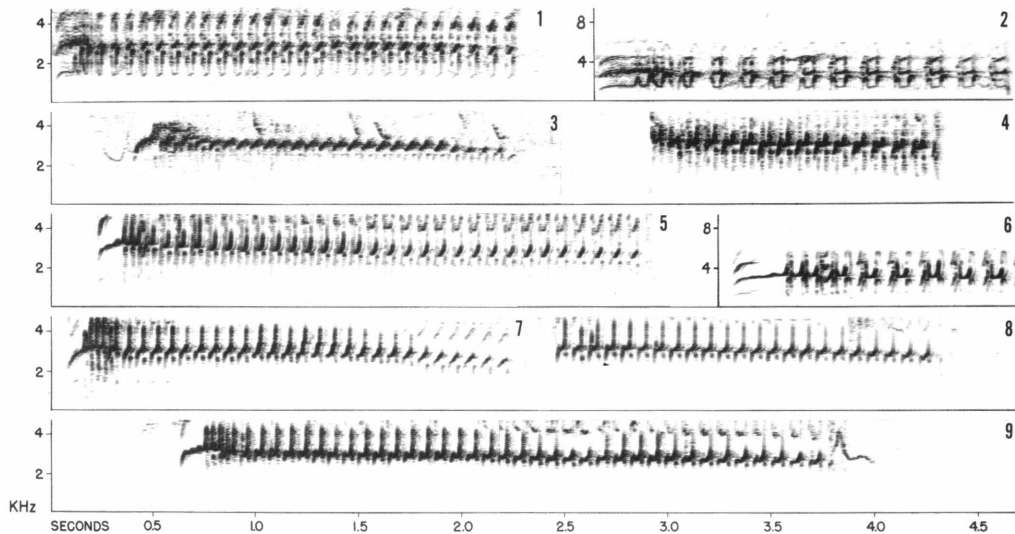


FIG. 68. Variation in vocal characters of *Myiarchus ferox*: rattles. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. f. ferox* (Peru, 1-3; Surinam, 4); *M. f. brunnescens* (Venezuela, 8, 9); intergrades between *M. f. ferox* and *M. f. brunnescens* (Venezuela, 5, 6; Colombia, 7). Spectrograms 2 and 6 were made from same recordings as were 1 and 5, respectively, but played at half normal speed; time scale for 2 and 6 is 2× that indicated.

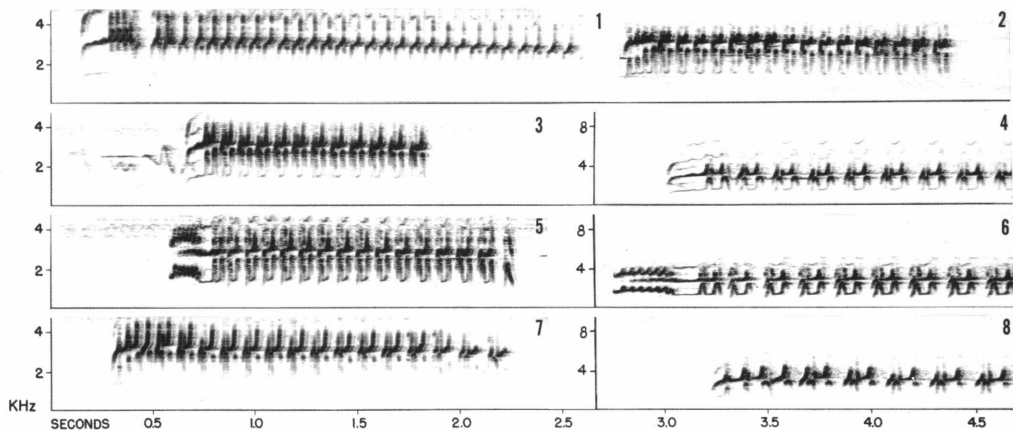


FIG. 69. Variation in vocal characters of *Myiarchus ferox*: rattles. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. f. brunnescens* (Venezuela, 1); *M. f. australis* (Argentina, 3-6; Brazil, 7, 8); intergrades between *M. f. ferox* and *M. f. australis* (Bolivia, 2). Spectrograms 4, 6, and 8 were made from same recordings as were 3, 5, and 7, respectively, but played at half normal speed; time scale for 4, 6, and 8 is 2× that indicated.

- 1972—November 5-8, with *ferox* near Tingo María, Huánuco, Peru; November 12-13, with *ferox* near San Ramón, Junín, Peru; November 21, with *ferox* near Quillabamba, Cuzco, Peru.
 1974—October 19-26, with intergrades between *ferox* and *australis* at Villa Tunari, Cochabamba, Bolivia.

SYSTEMATICS

Myiarchus ferox ferox (Gmelin)

- Muscicapa ferox* Gmelin, 1789, p. 934 (type locality, Cayenne, French Guiana; based primarily on "Le Tyran de Cayenne," Brisson, 1760, p. 398).
Myiarchus ferox: Tschudi and Cabanis, 1846, p. 153 (new combination).
Myiarchus ferox ferox: Berlepsch, 1907, p. 477. Oberholser, 1918, p. 304. Todd, 1922, p. 197. Hellmayr, 1927, p. 176 (synonymy). Zimmer, 1938a, p. 11. Pinto, 1944, p. 172. Phelps and Phelps, 1963, p. 190 (in part).

DIAGNOSIS: Rectrices and upper tail coverts not conspicuously fringed with Antique Brown, even in fresh plumage. Upperparts darker than in other two subspecies. Abdomen and under tail coverts yellow, with no brownish wash.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 70): Virtually the entire Amazon basin, from the eastern slopes of the Andes in southern Colombia, Ecuador, Peru, and northern Bolivia, eastward to the coast of the Guianas and Brazil.

Sympatric with *M. swainsoni*, *M. tyrannulus*, and *M. tuberculifer* throughout most of the range.

Earlier reports of this form on Trinidad (Roberts, 1934; Belcher and Smooker, 1937) can probably be explained by confusion with wintering specimens of *M. s. swainsoni*, as suggested by Junge and Mees (1958). I know of no specimen of *M. ferox* from Trinidad.

Specimens examined, 522; localities, by country, from north to south and west to east (see fig. 70; asterisks denote author's study areas): VENEZUELA, Boca del Río Amacuro, Delta Amacuro. GUYANA, Arunamai River; Georgetown. SURINAM, *Zanderij (Paramaribo; Republiek; Suriname River); Tapanahoni River. FRENCH GUIANA, Mana;

Cayenne; Approuague; Pied Saut. COLOMBIA, Morelia, Caquetá (Montañita); Mocoa, Putumayo (San Antonio); Río Churuyacu, Nariño (Río San Miguel). BRAZIL, Boca do Rio Branco, Amapá (Ferreira Gomes; Rio Amapari; Rio Tracajatuba); Caviana, Pará; Serra Curicuriari, Amazonas (Yucabí); Santa Isabel, Amazonas (Yavanari; Ilha do Santa Maria); Bom Jardim, Pará; Jacaré, Pará (Rio Trambetas); Mirapenima, Amazonas (Tauapessaçu); Faro, Pará; Obidos, Pará (Lago de Cuipéua); Santarém, Pará (Rio Tapajóz; Igarape Brabo; Pinhy); Fazenda do Rio Curuá, Pará; Tapará, Pará (Rio Xingú; Villarinho do Monte); Benevides, Pará; Belém, Pará; Ilha do Mangunça, Maranhão; Manãos, Amazonas (Cacao Pereira); Villa Bella Imperatriz, Amazonas; Tauary, Pará (Caxiricatuba); Baião, Pará; São Luiz, Maranhão (São Bento); Lago do Tefé, Amazonas (Santo Isídoro); Manacapurú, Amazonas; Itacoatiara, Amazonas; Rosarinho, Amazonas (Borba; Santo Antonio de Guajará); Igarape Boiussu, Pará; Baturité, Ceará; João Pessoa, Amazonas; Araguatins, Goiás; Therezina, Piauí; Serra Norte, Pará; Tabocas, Maranhão; Mamanguape, Paraíba; Santa Cruz, Amazonas; Hyutanahan, Amazonas; Calama, Amazonas; Brejo, Pernambuco; Rio Liberdade, Mato Grosso; Palmares, Pernambuco; Nova Olinda, Acre; Alto Xingú, Mato Grosso; Santa Rita do Rio Preto, Baía; Rio Suya-missú, Mato Grosso; Orobó, Baía (Andaraí); São Salvador, Baía; Cajazeiras, Baía (Jequié). ECUADOR, Papallacta, Napo (Cuyuja); San José, Napo (Río Cotapino); Zamora, Zamora Chinchipe (El Porotillo San José, Loja). PERU, Boca del Río Curaray, Loreto; Iquitos, Loreto (Puerto Indiana); Nazaret, Amazonas; Moyobamba, San Martín (Rioja); Sarayacu, Loreto; Saposoa, San Martín (El Tingo de Saposoa); Yarinacocha, Loreto; *Tingo María, Huánuco; Río Pachitea, Huánuco; Puerto Yessup, Pasco; Santa Rosa, Junín (Río Tambo); *San Ramón, Junín (San Juan; Oxapampa); Manú, Madre de Dios; Río Tambopata, Madre de Dios; *Quillabamba, Cuzco (San Fernando); Luisiana, Ayacucho; Quince Mil, Cuzco (Marcapata); Candamo, Puno. BOLIVIA, Río Mamoré, El Beni; Río Iténez, El Beni; San Joaquín, El Beni.

Myiarchus ferox brunnescens

Zimmer and Phelps

Myiarchus ferox brunnescens Zimmer and Phelps, 1946, p. 11 (type locality, Guasualito, Apure, Venezuela; holotype in Phelps Collection, on deposit in the American Museum of Natural History, examined). Todd, 1952, p. 294. Phelps and Phelps, 1963, p. 189.

DIAGNOSIS: Upperparts lighter and browner than in *ferox*. Gray of throat and breast and yellow of abdomen and under tail coverts suffused with a brownish wash. In fresh plumage, rectrices and upper tail coverts conspicuously fringed with Antique Brown; fringing of the upper tail coverts often retained even in worn breeding plumage.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 70): Restricted to a narrow belt of the llanos of southwestern Venezuela, from Táchira (Santo Domingo) and Portuguesa (Guanare) in the west to northwestern Bolívar (Río Cuchivero and Altagracia) in the east, and in extreme northeastern Colombia (Boyacá and Arauca).

Sympatric with *M. tyrannulus* and *M. tuberculifer* throughout much of its range.

Specimens examined, 43; localities, by country, from west to east (see fig. 70; asterisks denote author's study areas): VENEZUELA, El Sombrero, Guárico; Guanare, Portuguesa; *Barinas, Barinas; *San Fernando de Apure, Apure (Biruaca; Río Guárico; Río Apure Seco; Camaguan, Guárico); Cabruta, Guárico (Caicara, Bolívar); Altagracia, Bolívar; *Río Chururu, Táchira (Santo Domingo); Guasualito, Apure; Caño Guaniamo, Bolívar; Las Bonitas, Apure. COLOMBIA, Río Cóbogon, Boyacá; Ceiba, Arauca.

MORPHOLOGICAL INTERGRADATION BETWEEN *brunnescens* AND *ferox*

The relatively recent recognition of *brunnescens* in the Apure watershed of southwestern Venezuela delayed an accurate interpretation of peripheral populations that are intermediate between *brunnescens* and nominate *ferox*. The Phelps' collectors did not take their first specimens from Apure until

1939; these and subsequent collections led to the description of *brunnescens* in 1946. Prior to 1946, workers had consistently though reluctantly assigned Venezuelan specimens from the Orinoco drainage to the east and from Meta, Colombia (also within the Orinoco watershed) to *australis*, the southern subspecies (Todd, 1922; Hellmayr, 1927; Zimmer, 1938a, 1938b). Hellmayr (1927) remarked that "the birds occurring in the Orinoco-Caura basins are so close to *M. f. australis* of southern Brazil, that I do not venture to separate them, in spite of the fact that their ranges are divided by the interposition of the much darker *M. f. ferox*." On the basis of a difference in the timing of the molt in the northern and southern populations, Zimmer (1938b) discounted the possibility that this northern population of *australis* might in reality consist of wintering birds of a migratory portion of the southern subspecies. He commented that "obviously the northern birds are not migrants from the south in spite of the great similarity in appearance and in spite of the fact that there is a different subspecies in the intermediate region." When Zimmer and Phelps (1946) described *brunnescens*, they acknowledged that specimens from peripheral areas in the Orinoco drainage "are intermediates but a little closer to *M. f. brunnescens*," and then added that "*australis* has been collected to the east of the new race in the State of Guarico and in the Caura valley." Todd (1952) interpreted the latter statement to mean that Zimmer and Phelps regarded *australis* in Venezuela to be "a winter migrant from beyond the Equator," in spite of Zimmer's (1938b) previous statement to the contrary. Todd was no doubt influenced by the first Venezuelan checklist, in which Phelps and Phelps (1950) did in fact list *australis* as a migrant from the south, on the basis of specimens from the Lower Orinoco and Caura region. Phelps and Phelps retained this interpretation in their revised checklist (1963), but added that "the status of *australis* in Venezuela requires further study." But in notes made during the 1950s, in preparation for a manuscript for Peters's Checklist, Zimmer was clearly aware that the supposed northern population of *australis* was in

reality the result of intergradation between *ferox* and *brunnescens*, and he reserved the name *australis* for the nonmigratory southern subspecies.

The geographical region involved in the zone of intergradation between *ferox* and *brunnescens* is an extensive one (see fig. 70) and is considerably larger than the range of *brun-*

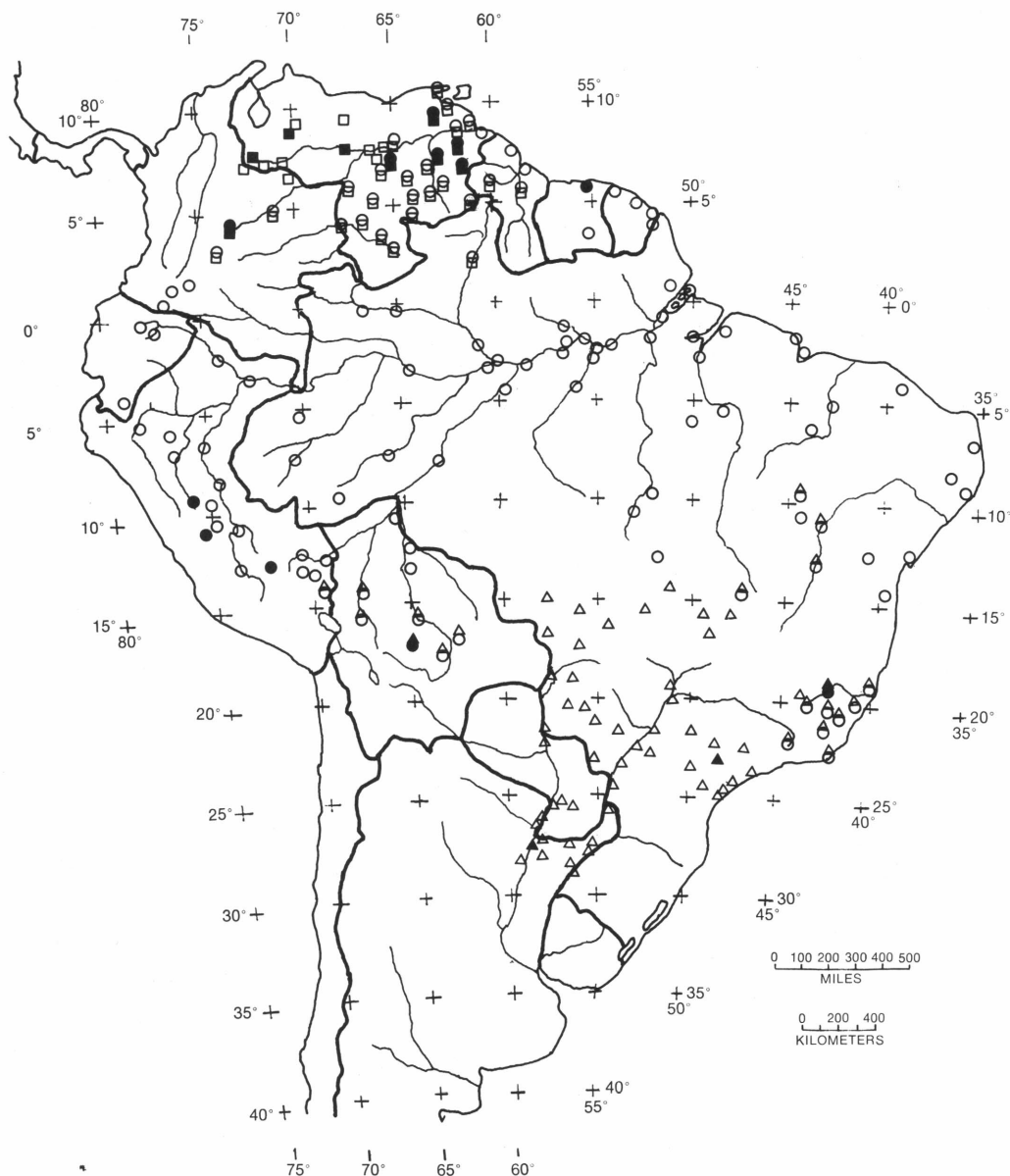


FIG. 70. Distribution of *Myiarchus ferox* as indicated by localities of specimens examined (open symbols) and by sites where author studied this species in the field (solid symbols). The three subspecies are *ferox* (circles), *brunnescens* (squares), and *australis* (triangles). Zones of intergradation between subspecies are indicated by specimen localities marked with combinations of two of these three symbols. See text for lists of these localities and page 571 for an itinerary of author's fieldwork with this species.

nescens itself, since I prefer to restrict the latter to that originally proposed by Zimmer and Phelps (1946). Todd (1952) fully appreciated the extent of the area in which birds could not readily be assigned to either *ferox* or *brunnescens*, and chose to recognize formally the intermediate population under the name *orenocensis*. Like Zimmer before him, Todd correctly argued that his Orinoco specimens could not be migrants from the southern *australis*, because many of them had been collected at a time when *australis* was known to be breeding. Zimmer synonymized Todd's *orenocensis* under nominate *ferox* in his manuscript for Peters's Check-list. To do that, however, increases the range of variation in plumage coloration of nominate *ferox* to such an extent that it would also include the characteristics of the southern *australis*. I prefer to treat these morphological intermediates in the north as intergrades between *ferox* and *brunnescens*, without giving them a name, and to emphasize that many specimens are not separable from *australis* other than on the basis of a different timing of their annual cycle.

The specimens that I have been unable to assign with certainty to either nominate *ferox* or to *brunnescens*, and which are the basis for the zone of intergradation as indicated in figure 70, are listed below. All are too brown above for nominate *ferox*, but too yellow below for *brunnescens*; some even have a suggestion of the fringing of the rectrices with Antique Brown seen in *brunnescens*; none have a brownish wash on the underparts to the degree typical of *brunnescens*. These are the same characteristics that would make separation of these specimens from *australis* extremely difficult, were it not for an important difference in the timing of the prebasic molt.

Intergrades between *ferox* and *brunnescens* have a molt schedule that is either identical with that of *brunnescens* or intermediate between that of *brunnescens* and that of nominate *ferox*. None exhibit a molt schedule like that of nominate *ferox* and of *australis*.

Delta region of the Orinoco (Delta Amacuro, Sucre, and Monagas): PC 1321-1323, 23805, 48205, 49925, 49927, 67549; ANSP 58479, 58480; AMNH 67008. Three of these specimens had at one time been identified as "*australis*," reflecting

their intermediate characteristics. PC 23805 is representative of this particular series of intergrades: taken at Yaguaraparo, Sucre, which falls within the range of nominate *ferox* as designated by Zimmer (MS) and by Phelps and Phelps (1963), on September 23, 1943 (at a time when nominate *ferox* is in worn to very worn plumage and breeding); this specimen is in late stages of prebasic molt and hence is in fresh plumage, which corresponds well with the timing of the molt in *brunnescens*; the plumage is too brown for *ferox*; rectrices with conspicuous edging of Antique Brown; but too dark above and too yellow below, with insufficient brownish wash on the underparts, to be *brunnescens*.

Guyana: ANSP 51378. Taken at Bartica Grove on January 15, 1880; this specimen is in fresh plumage (molt complete) at a time when nominate *ferox* would either be in very worn plumage or would exhibit prebasic molt.

Eastern Bolívar (Ciudad Bolívar and eastward) and Rio Branco, Brazil: PC 16320, 16321, 16325-16327, 17596, 24346, 30424, 44833, 46411; AMNH 177697, 323846, 73727. These specimens exhibit the molt schedule of *brunnescens*; seven of them at one time had been identified as "*australis*"; Todd (1952) remarked: "Dr. Zimmer placed British Guiana birds with *ferox*, but our two specimens from El Callao, on the Guiana frontier [of Venezuela], clearly belong to the present race [his new subspecies, *orenocensis*]. Obviously, also, the middle Orinoco birds are not *brunnescens*, to judge from the description of that race and from the single specimen before me from the Apure which corresponds to that description. As already said, the new race is barely separable by its characters from *australis*"; AMNH 236864, taken at Caracahy, Rio Branco, on August 29, 1927, is in early stages of molt and hence the plumage is much too worn to be useful for any critical color comparisons, but the molt schedule is that of *brunnescens* rather than that of *ferox* or *australis*.

Western Bolívar, Anzoátequi, and Territorio Amazonas: PC 12809, 21964, 21965, 25772, 39565, 39566, 39568, 42497, 52657, 52662, 66861, 66902, 66903; AMNH 75565, 75566, 75569, 120856, 120857, 274357, 274358, 274360, 274361, 274363, 294707, 433241, 274361, 433243-433245, 435781, 497300, 497306. These specimens exhibit the molt schedule of *brunnescens*; 22 of them had been identified as "*australis*" at one time. AMNH 497300 was taken at Perico (= Puerto Ayacucho), Amazonas, on November 22, 1898 and is in fresh plumage and is

intermediate in coloration; at one time it was identified as "*australis*" but later assigned to *brunnescens*. Zimmer (MS) indicated that this specimen is "hardly referable to *brunnescens* but more so than to any other forms." AMNH 497306 was taken at La Prisión, Venezuela (lower Caura valley) on December 13, 1900; it had been tentatively identified originally as *venezuelensis*, because of some Antique Brown edging on the rectrices, though it does not agree with that species in other characters; Zimmer had identified it as "*australis*" at one time.

Meta, Colombia: AMNH 122336, 122338-122340, 308690, 460504-460506; FMNH 297614-297616, 297619-297621, 298073; ANSP 159166, 159173. Zimmer had commented (MS) that the specimens from Villavicencio, Meta, "are hardly referable to *brunnescens* but more so than to any other forms." These specimens suggest an annual cycle that is intermediate between that of *ferox* and that of *brunnescens*; five had been identified as "*australis*," the rest as *brunnescens* or *ferox* ssp. The series of Field Museum of Natural History specimens from Carimagua, Meta, includes males taken in October and November, with small testes, and both sexes in February with enlarged gonads. I collected five specimens near Villavicencio in late May; all were in molt, and four show either mid- or late-stages of replacement of the remiges. I found the Meta population only moderately responsive to playback in late May, whereas Frank Gill (personal commun.) found this population to be very responsive in February. These data suggest that breeding occurs from January through March, followed by the prebasic molt from March through June.

Specimens of intergrades between *brunnescens* and *ferox* examined, 165; localities, by country, from north to south and west to east (see fig. 70; asterisks denote author's study areas): VENEZUELA, Yaguaraparo, Sucre; Pedernales, Delta Amacuro (Boca Uraco; Río Mánamo); *La Morrocuya, Monagas; Caño Dabomana, Delta Amacuro (Jobure); Sacupana, Delta Amacuro (Piacoa; Río Toro); Barrancas, Anzoátegui (Río Suata); *El Palmar, Bolívar; El Manteco, Bolívar; *Maripa, Bolívar (La Prisión; La Unión); La Paragua, Bolívar (Cerro Tigre; Salto Uraima); *Tumeremo, Bolívar (El Callao; Guasipati; El Dorado); Raudal Alto, Bolívar; Salto Pará, Bolívar (Raudal Guaiquinima; Urimán); Cerro Auyan-tepui, Bolívar;

Puerto Ayacucho, Amazonas; Boca del Río Chanaro, Bolívar; Caño Antabari, Bolívar (Erebenequén; Salto Maisa); San Juan de Manapiare, Amazonas; Santa Teresa, Bolívar (Río Icabarú); Sabana Kirichú, Bolívar; Las Carmelitas, Amazonas (Puerto Yapacana); San Fernando de Atabapo, Amazonas; Cerro Duida, Amazonas (Esmeralda; Tamatama); Boca del Río Ocamo, Amazonas. GUYANA, Mazaruni River; Bartica Grove (Kartabo; Rockstone; Essequibo River). COLOMBIA, Carimagua, Meta; *Villavicencio, Meta (Los Micos; Río Guatiquía; Río Ocoa); Cordillera de la Macarena, Meta (Río Duda). BRAZIL, Caracarahy, Rio Branco.

RELATIONSHIP OF

brunnescens WITH *Myiarchus venezuelensis*

I have discussed elsewhere (p. 495) the relationship of *M. venezuelensis* and *M. ferox*, and have established the previously unknown sympatry between these two species. Though the populations of *M. ferox* involved at the known localities of sympatry in eastern Venezuela are best characterized as intergrades between *brunnescens* and nominate *ferox*, there is the possibility of further sympatry with *M. venezuelensis* along the northern border of the range of *brunnescens* and particularly in the Venezuelan states of Lara, Yaracuy, and Carabobo.

Since *brunnescens*, and all other populations of *M. ferox*, differ greatly from *M. venezuelensis* in vocal characters, it was not surprising to find that *brunnescens* can discriminate between its own repertoire and that of *M. venezuelensis*. This discriminatory ability is illustrated by a series of playback experiments with a territorial pair of *brunnescens* on the Río Chururu, Táchira, Venezuela, conducted on May 25, 1969:

Experiment 9—study area one, 340 m. Tapes used, *M. venezuelensis* vs. *M. swainsoni*. Birds silent, location unknown. Start at 8:25 A.M. No show during first half. Cable switch at 8:32. No show during second half, and no vocalizations heard outside the experimental area during this experiment.

Experiment 10—same locality, pair, and date as above. Tapes used, *M. venezuelensis* vs. *M. f. brunnescens*. Location of birds still unknown. Start at

8:43 A.M. One bird showed in *brunnescens* area within 1 minute, silent, 30 ft. from model. A second bird gave a rattle within experimental area, and the first bird flew over to the second, whereupon both birds flew out of area. Both birds back to within 50 ft. of *brunnescens* model at 8:48, bill snapping and giving rasping whistles. In to 30 ft. from model at 8:49, giving rasping whistles and moving about together in short chases within 30 ft. radius of the *brunnescens* model. Cable switch at 8:50. Pair moved to midpoint within 30 seconds, silent. Over to 20 ft. from new *brunnescens* model by 8:52. In a study, at 10 ft. from model. Both out to 40 ft. of model at 8:54, silent. Giving more rasping whistles at 8:54:30 at that location. A good rattle at 8:55. Both birds remained at about 40 ft. from *brunnescens* model until end of experiment, giving occasional rasping whistles.

Experiment 11—same locality, pair, and date as above. Tapes used, *M. tyrannulus* vs. *M. tuberculifer*. Birds silent again, location unknown at start at 9:05 A.M. No show during first half. Discontinued experiment at the cable switch.

Experiment 12—same locality, pair, and date as above. Tape used, *brunnescens* alone, to test stimulus value of this tape alone, after failure to respond in previous experiment. Birds still silent, location unknown at start at 9:15 A.M. The pair showed within 1 minute, giving rasping whistles and hiccup notes, and an occasional rattle. After 5 minutes of playback and recording of response, I collected both birds.

RELATIONSHIP OF

Myiarchus ferox AND *Myiarchus panamensis*

I have earlier (p. 562) pointed out that *M. ferox* is closest vocally to *M. panamensis*, a completely allopatric species found west of the Andes. Though there are prominent differences between the vocal repertoires of these two species that far exceed the usual differences between the voices of species of *Myiarchus*, I was curious to see what response I might get from territorial *panamensis* to the experimental playback of a *M. ferox* tape. A series of experiments made in Colombia and described on p. 562 illustrates the failure of *M. panamensis* to respond to playback of *M. ferox*. Likewise, a reconnaissance tape of *M. panamensis* proved to be of no value in locating pairs of *M. ferox*.

Myiarchus ferox australis Hellmayr

Myiarchus ferox australis Hellmayr, 1927, p. 177 (type locality, Agua Suja, near Bagagem, Minas Gerais, Brazil; holotype in the Munich Museum; synonymy). Zimmer, 1938a, p. 14. Pinto, 1944, p. 175.

Myiarchus cantans Pelzeln, 1868, pp. 117, 182 (in part).

Myiarchus ferox swainsoni: Berlepsch, 1907, p. 477. Oberholser, 1918, p. 307. Todd, 1922, p. 200 (synonymy).

DIAGNOSIS: Upperparts lighter and browner throughout than in *ferox*, and nearly as brown as in *brunnescens*. Underparts as in *ferox*, with abdomen and under tail coverts yellow and lacking a brownish wash as seen in *brunnescens*. Rectrices and upper tail coverts fringed with Antique Brown, in fresh plumage only, but less conspicuously than in *brunnescens*.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 70): Tropical zone of southern South America, between latitude 15° S and 30° S; southeastern Bolivia, southern Mato Grosso, southern Goiás, and southern Minas Gerais, southward through the drainages of the Paraguay, Paraná, and Uruguay rivers as far as southern Corrientes, Argentina, and extreme southwestern Rio Grande do Sul, Brazil.

Sympatric with *M. swainsoni* and *M. tyrannulus* through most of its range.

Resident throughout its range; there are large series of specimens taken from the breeding grounds in Argentina, Paraguay, and Brazil, in fresh plumage from May through August.

Specimens examined, 256; localities, by country, from north to south and west to east (see fig. 70; asterisks denote author's study areas): BRAZIL, Dumba, Mato Grosso; Tapiropan, Mato Grosso; Cuiabá, Mato Grosso (Chapada); Aragarcas, Goiás; Jaraguá, Goiás (Rio das Almas); Brasília, Distrito Federal (Planaltina); Rondonópolis, Mato Grosso; Descalvados, Mato Grosso; Nerópolis, Goiás; Rio Piquiri, Mato Grosso; Corumbá, Mato Grosso; Palmiras, Mato Grosso; Santana de Parnahyba, Mato Grosso; Lagôa Santa, Minas Gerais; Miranda, Mato Grosso; Salobra, Mato Grosso (Aquidauana); Itapurá, São Paulo; Campeiro,

Mato Grosso; Pôrto Quebracho, Mato Grosso; Vaccaria, Mato Grosso; Pôrto Eptácio, São Paulo; Lins, São Paulo; Pôrto Cabral, São Paulo; Bebedouro, São Paulo; Amambahy, Mato Grosso; Pôrto Marcondes, São Paulo (Rio Paranapanema); Socorro, São Paulo (Ribeirão Fundo); Pôrto Camargo, Paraná; *Fazenda Barreiro Rico, São Paulo (Anhembí; Victoria); Salto Grande, São Paulo; São Sebastião, São Paulo; São Paulo, São Paulo (Ipiranga; Pôrto Estrada; Primeiro Morro); Pôrto Britânia, Paraná (Guayrá); Itararé, São Paulo; Onça Parda, São Paulo (Juquiá); Registro, São Paulo; Itaqui, Rio Grande do Sul. PARAGUAY, Puerto Pinasco, Chaco; Sapucaí, Paraguairí (Escobar); Nueva Italia, Paraguairí; Villarrica, Guairá (Colonia Independencia). ARGENTINA, Puerto Segundo, Misiones (Puerto Aguirre; Arroyo Uruguay; Puerto Bertoní, Paraguay); Formosa, Formosa; Río de Oro, Chaco; Itatí, Corrientes; *Las Tres Marías, Corrientes (Corrientes; Resistencia, Las Palmas, and Río Guá, in Chaco); Ituzingó, Corrientes (Isla Apipé Grande); Bonpland, Misiones; Garuchos, Corrientes (San José and Concepción, Misiones); Manantiales, Corrientes; Ocampo, Santa Fé; Cuay Grande, Corrientes (Torrent); Alvear, Corrientes (Rio Aguapey; Itaqui, Rio Grande do Sul, Brazil).

REMARKS ON SOUTHERN LIMIT OF DISTRIBUTION

The southernmost populations of *australis* appear to be restricted to the riparian woodlands along the Paraná and Uruguay rivers, and I have seen specimens from as far south along the Rio Uruguay as Alvear, Corrientes, and Itaqui, Rio Grande do Sul. The literature (Todd, 1922; Hellmayr, 1927; Zimmer, 1938a; Olog, 1963; Meyer de Schauensee, 1966) has this form ranging southward into Uruguay, and as far as the province of Buenos Aires in Argentina, presumably due to the confusion and ambiguity often associated with the distinction between *M. ferox australis* and *M. s. swainsoni* and *M. s. ferocior*. I have seen no specimens of *australis* from Uruguay, including the collections made available to me in Montevideo. Cuello and Gerzenstein (1962) had included *australis* in their checklist of Uruguayan birds

on the basis of "sight records" only (Cuello, personal commun.; Aplin, 1894). If this form is ever collected in Uruguay, it almost surely will be found along the Rio Uruguay in the extreme northwestern corner.

Olog (1963) gave the range of *australis* as extending westward in Argentina to Tucumán and Córdoba. There are no specimens of *australis* from either of these provinces in the collections of the Museo Argentino de Ciencias Naturales in Buenos Aires, the Instituto Miguel Lillo in Tucumán, or the Museo de La Plata in La Plata. The basis for the Tucumán record was undoubtedly Wetmore (1926), who reported on a series of *M. swainsoni ferocior* taken a number of years prior to the original description of *australis*. The Córdoba record was based on a misidentified specimen of *ferocior* taken by Partridge (1953) at Puesto Los Sauces, Córdoba. To my knowledge, the only specimens of *australis* from Argentina, other than those from Corrientes and Misiones, were taken just west of the Paraná river in the provinces of Santa Fe, Chaco, and Formosa. In view of the mesic habitats occupied by *australis* in Corrientes, it would be surprising to find this form any appreciable distance westward from the Río Paraná, in the chaco region.

MORPHOLOGICAL INTERGRADATION BETWEEN *australis* AND *ferox*

The zone of intergradation between *australis* and nominate *ferox* has been well documented only in central Bolivia and in eastern Brazil, where it extends from southern Piauí to Rio de Janeiro. There has been little collecting in much of the intervening region of Mato Grosso (fig. 70).

Specimens of intergrades between *australis* and *ferox* examined, 97; localities, by country, from north to south and west to east (see fig. 70; asterisks denote author's study areas): BRAZIL, Patos, Piauí; Barro do Rio Grande, Baía; Bom Jesus da Lapa, Baía; São João da Aliança, Goiás; *Ipatinga, Minas Gerais (Rio Doce; Barra do Piracicaba; São José da Lagôa; Lagôa Juparanã, Espírito Santo; Mariana, Minas Gerais; Raul Soares, Minas Gerais; Santa Teresa, Espírito Santo (Jatiboca); Serra do Caparaó, Espírito Santo; Volta Grande,

Minas Gerais; Baependi, Minas Gerais; Cabo Frio, Rio de Janeiro. PERU, Huacamayo, Puno (Sandia). BOLIVIA, Susi, El Beni; Guanay, La Paz (Río Mapiri); Boca del Río Chapare, Cochabamba; Palmerito, Santa Cruz (Río

Quizer); *Villa Tunari, Cochabamba (San José; Palmar; Todos Santos; Tres Arroyos; Yungas de Cochabamba); Buena Vista, Santa Cruz (Río Surutú; Sara; San Carlos).

MYIARCHUS SEMIRUFUS SCLATER AND SALVIN

The known range of this well-marked monotypic Peruvian endemic is limited to a narrow zone along the coast of northwestern Peru—one of the most restricted ranges of any species in the genus (fig. 71). The species is nonmigratory.

Because of the unique coloration of the plumage, Bangs and Penard (1921) assigned *semirufus* to a new, monotypic genus, *Muscifur*. Subsequent authors have generally retained *semirufus* in *Myiarchus* (Todd, 1922; Hellmayr, 1927; Zimmer, 1938a), and my field observations on behavior and breeding biology support this view (Lanyon, 1975a).

DIAGNOSIS: The predominantly Cinnamon underparts and the amount of Antique Brown in the wings and tail set this species apart from all other species of *Myiarchus*. The underparts are nearly uniform Cinnamon throughout, in contrast to the gray and yellow or white coloration of all other species. In fresh specimens, mandible black throughout and color of mouth lining pale Orange Yellow.

Vocal response to intruding conspecifics consists of rasping whistles, with frequencies mostly above 3 kHz. and never below 2 kHz., and *no* rolls. Dawn song includes isolated "huit" notes and rasping whistles, modulated at a frequency of 45 to 60 Hz.

HABITAT (FIG. 72): The distribution of the species is entirely within but does not occupy all of those Peruvian life zones identified by Tosi (1960) as tropical and subtropical desert and thorny desert. The localities where I was most successful in locating *semirufus* were open thorn-woodlands dominated by mesquite (*Prosopis* spp.) and acacia (*Acacia* spp.) trees. Often the trees were widely separated from one another by a sparse groundcover of grasses and herbs. Koeppke (1970) characterized the species as "typical of the xerophytic steppes and mesquite savannahs." For a more detailed descrip-

tion of the habitat of *semirufus*, see Lanyon (1975a).

Except at the extreme northern end of its range, *semirufus* is not sympatric with other *Myiarchus*. It is not found far enough up the Andean slopes to overlap with *M. tuberculifer*. Locally in the northern departments of Piura and Tumbes, *semirufus* may occur in the same open thorny woodland as *M. phaeocephalus*.

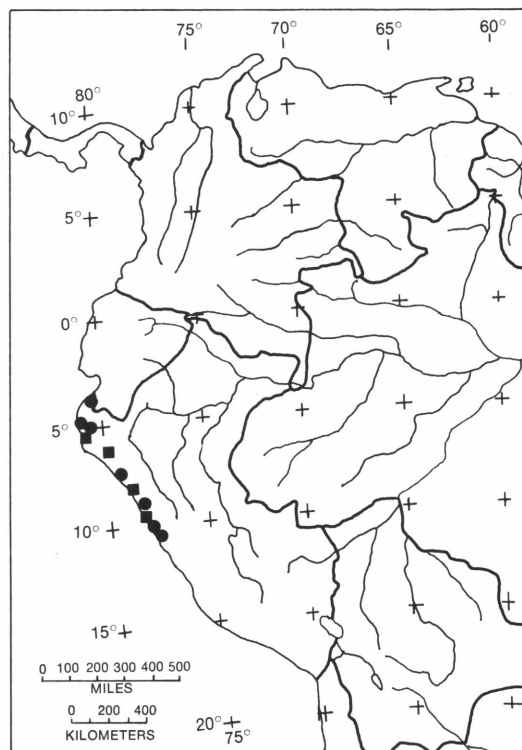


FIG. 71. Distribution of *Myiarchus semirufus* as indicated by localities of specimens examined (circles) and by sites where author studied this species in the field (squares). See page 586 for a list of these localities and for an itinerary of author's fieldwork with this species.

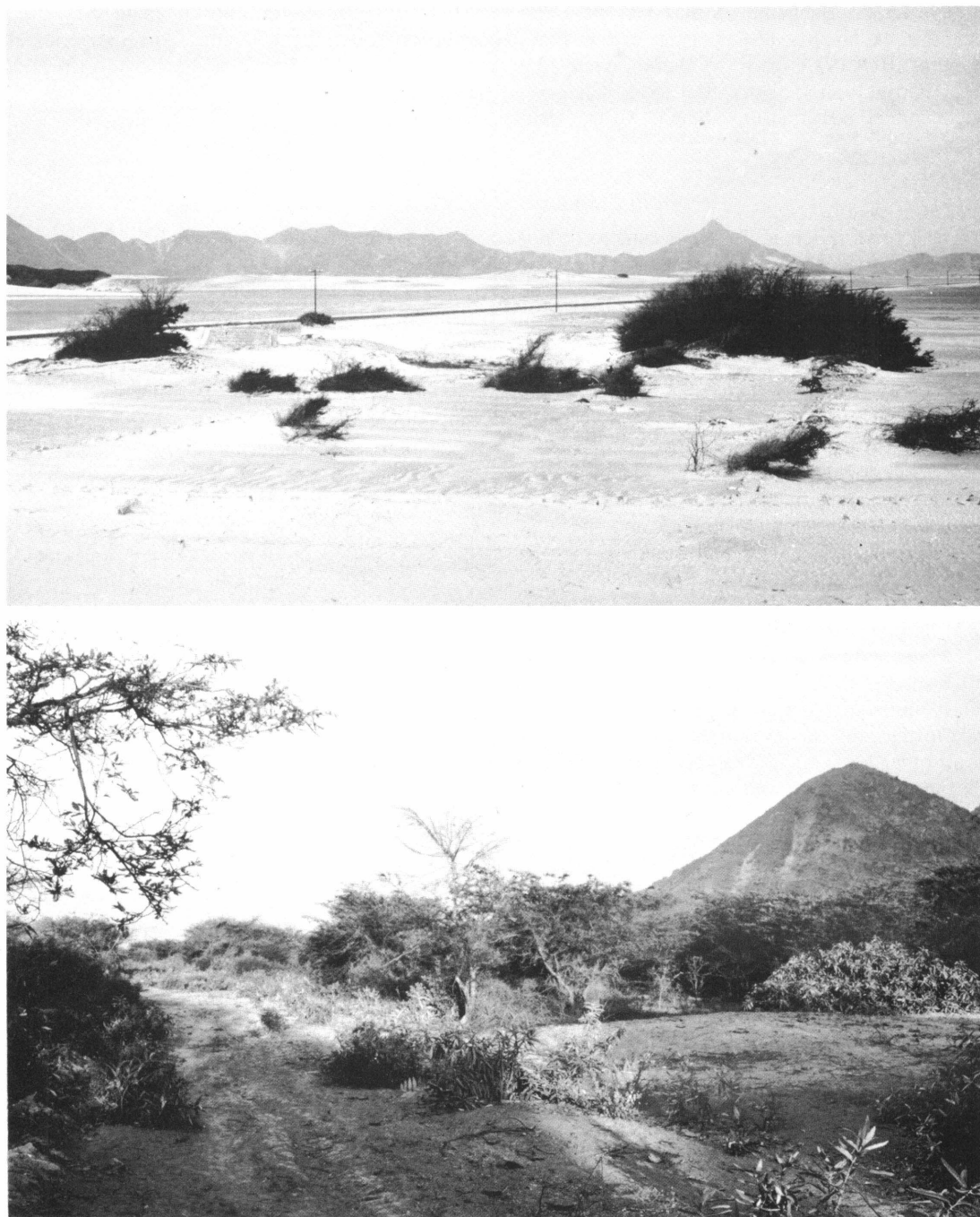


FIG. 72. Habitat of *Myiarchus semirufus*. *Top*: Tropical desert, about 50 km. south of Chimbote, Department of Ancash, Peru. A nest of this species was found in large clump of *Acacia macracantha*, center right. *Bottom*: Open thorn woodland about 25 km. south of Chimbote, Peru, where the species was recorded and collected in December 1973; elevation near sea level.

BREEDING AND ANNUAL CYCLE: For a detailed account of the location and description of the only known nest of *Myiarchus semirufus* see Lanyon (1975a).¹ In summary, on December 25, 1973, I found a nest in a large clump of *Acacia macracantha* at a locality about 50 km. south of Chimbote, Department of Ancash, Peru (fig. 72). The nest, about 1 m. above-ground, was well hidden in a darkened recess

¹After this manuscript had gone to press I received the details of a second nest, discovered by Theodore Parker on May 15, 1978, 10 km. NE of Ñaupe, Department of Lambayeque, Peru. This nest was 140 mm. below the entrance of a tree cavity, made of fur, lined with bits of plastic, snakeskin, and several feathers and contained three downy young and one egg. The attendant adult male was already in molt. This important record confirms my supposition that the species will utilize cavities, when available, in the typical manner of *Myiarchus*, and that the breeding season in the northern part of the species' range is significantly later in the season than in the southern part.

in the acacia (fig. 73). Though the nest was an open cup and not situated in a tree cavity in the typical manner of *Myiarchus*, the light intensity at the nest was extremely low due to the impenetrable mass of dead branches and accumulated litter from the foliage of previous growing seasons. The nest was lined with fine and coarse fur, numerous pieces of shed reptilian skin, fragments of tissue paper, newspaper, and clear plastic, and a few white feathers. The three eggs had been incubated for about two days when collected on December 26. In size, shape, ground color, and markings they are well within the range of variation one finds among the eggs of *Myiarchus*.

The observation above and the data from molting birds suggest that in the southern part of its range (Departments of Ancash and La Libertad) *Myiarchus semirufus* breeds in December and January. At the northern end of the range, in Piura and Tumbes, the species proba-



FIG. 73. *Myiarchus semirufus*, lower center, perches on edge of its well-concealed nest, surrounded by dead branches and accumulated litter of acacia foliage from previous growing seasons. Photograph taken with a 300 mm. lens at a distance of 11 m., December 26, 1973; elevation near sea level.

bly breeds from one to two months later, judging from the dates of specimens taken in molt. This asynchrony in the breeding cycle is undoubtedly due to differences in the timing of the scant precipitation in this arid region and the resulting variations of the vegetation and insect populations (Lanyon, 1975a).

The definitive plumage is renewed during a complete prebasic molt following breeding. Specimens collected in the southern part of the range from February through April show various degrees of replacement of the flight feathers, while others taken as early as March and April are in fresh plumage. Specimens from the northern part of the range show molt in the wings and tail in April and May, and there are fresh plumaged specimens in June. A juvenile that I collected in Ancash, Peru, on March 4, 1973, had not begun its first prebasic molt.

VOCAL CHARACTERS: The analysis of vocal characters of *M. semirufus* is based on recordings of four pairs in Ancash, Peru.

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 74 and 75.

In response to playback, or when excited by intruding conspecifics, *M. semirufus* vocalizes with repeated rasping whistles and hiccups. The rasping whistle (fig. 74: 13-22; fig. 75:1,5) is given either as an isolated call or, in situations of more intense stimulation, in rapid sequence. The carrier frequency begins at an extremely high pitch (4 kHz.), for *Myiarchus*, and descends a full kilohertz. It is modulated at frequencies of from 45 to 60 Hz., but with relatively little deviation from the carrier frequency. Often a bird will give a rasping whistle followed immediately by a hiccup (as in fig. 74:20-22). The latter call also is high-pitched, compared with other *Myiarchus*, and is derived from modifications of the "huit" note. Generally, it is a call of two syllables, each of which is a prominent glissando, though occasionally it will consist of three "huit"-like notes (fig. 75:6-8). The occasional "huit" note and rasp may be included as well, but these are not prominent in the vocal response to playback. The rasp, not illustrated here (but see Lanyon,

1975a, p. 451), is not unlike its counterpart in the repertoires of other species of *Myiarchus*.

Foraging birds not excited by playback or intruding conspecifics will deliver "huit" notes (fig. 74:7-12) at irregular intervals. The "huit" call produces a chevron-like trace that is normally continuous in energy, but occasionally is discontinuous (fig. 74:9). Typically, it is given with minimum amplitude and hence does not carry far. Another call given under similar circumstances is a virtually unmodulated whistled note (fig. 75:2-4) that descends a full kHz. in less than 0.25 second. This is virtually the same carrier frequency that, when modulated at a moderate rate, becomes the rasping whistle during times of greater stimulation. These descending whistled notes may be rendered either singly or in short series and, along with the isolated "huit" notes, presumably serve as location notes in the communication between paired birds. When the incubating female left the one nest that I located, she was joined by her mate and the pair foraged together. Unmodulated descending whistles were the only vocalizations used by the pair at this time. The only reference in the literature to the voice of *M. semirufus* is Taczanowski's (1884) quotation from the field notes of Jelski: "Its voice is a monotonous whistle, repeated from time to time." Presumably the reference is to this descending whistle.

DAWN SONG: The dawn song of the male *M. semirufus* consists of alternated renditions of "huit" notes and rasping whistles (fig. 74:1-3), with frequent interjections of a more complex phrase derived from a combination of a modified hiccup note and a simple descending whistle (fig. 74:4-6). This complex phrase is given less frequently than the other components of the dawn song, and normally follows in rapid sequence the rendition of either a "huit" note or a rasping whistle. The "huit" notes and rasping whistles of dawn song do not differ from those given during the daylight hours other than in the regular frequency with which they are given per unit time. A normal sequence of components in a dawn song might include alternating renditions of "huit" notes and rasping whistles for 10 or 15 seconds, and then a complex component introduced by a

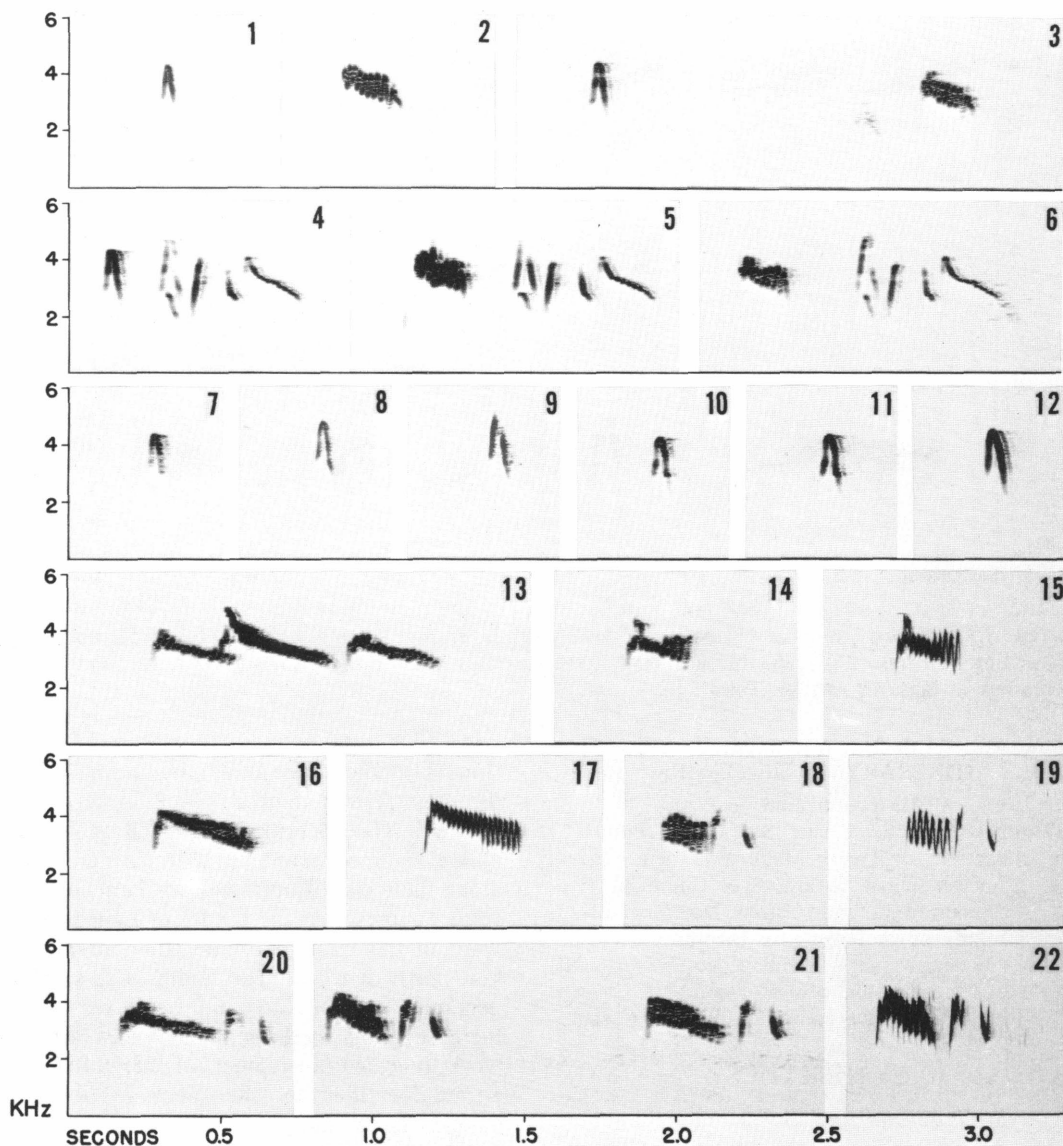


FIG. 74. Variation in vocal characters of *Myiarchus semirufus*: dawn song (1-6), "huit" notes (7-12), rasping whistles (13-19), and combinations of rasping whistles and hiccups (20-22). Spectrograms were made from recordings of birds in Ancash, Peru. 300 Hz. filter was used for 15, 17, 19, and 22 only.

rasping whistle. After another sequence of alternated "huit" notes and rasping whistles, a complex component introduced by a "huit" note might follow.

GEOGRAPHICAL VARIATION: Since all of my recordings were made in the Department of Ancash, Peru, I have no basis for discerning geographical variation in this species.

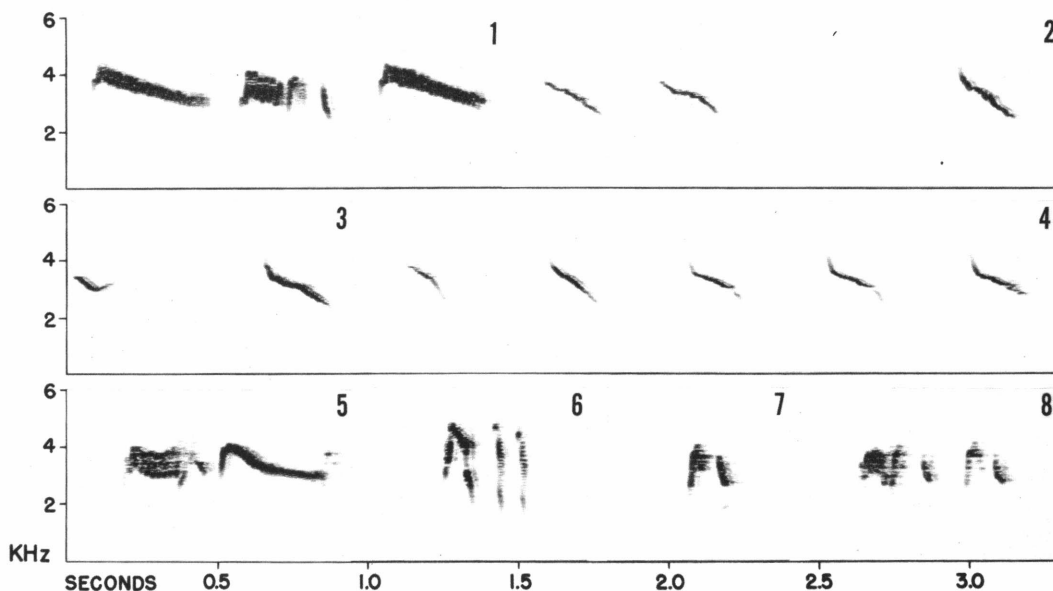


FIG. 75. Variation in vocal characters of *Myiarchus semirufus*: rasping whistles (1 and 5), unmodulated descending whistles (2-4), and hiccups (6-8). Spectrograms were made with 45 Hz. filter and are from recordings of birds in Ancash, Peru.

ITINERARY OF FIELDWORK

All localities are in Peru.

1973—February 26-27, near San Lucas, Piura (23 km. NE of Paita); March 3-4, near Casma, Ancash (about 50 km. S of Chimbote); December 19-20, near Casma; December 21-23, 5 kms. N of Paiján, La Libertad; December 23, near Jayanca, Lambayeque (50 kms. NE of Chiclayo, and also 10 kms. N of Chepén, La Libertad; December 24-29, near Casma.

SYSTEMATICS

Myiarchus semirufus Sclater and Salvin

Myiarchus semirufus Sclater and Salvin, 1878, p. 138 (type locality, Pacasmayo, Peru; holotype in Steere Collection, University of Michigan). Taczanowski, 1884, p. 325. Sclater, 1888, p. 263. Berlepsch, 1907, p. 478. Todd, 1922, p. 183. Hellmayr, 1927, p. 187 (synonymy). Zimmer, 1938a, p. 25. Bond, 1947, p. 139. Meyer de Schauensee, 1966, p. 349; 1970, p. 298. Koepcke, 1970, p. 96.

Muscifur semirufus: Bangs and Penard, 1921, p. 376 (new combination).

DISTRIBUTION AND SPECIMENS EXAMINED

(FIG. 71): The range of *M. semirufus* is one of the most restricted of all South American *Myiarchus*. The localities at which it has been collected or observed are all in a narrow zone along the coast of northwestern Peru, extending from Tumbes near the border of Ecuador southward to the vicinity of the Río Pativilca, 200 km. north of Lima. The width of this range is generally less than 50 km., being restricted on the east by the foothills of the Andes. My fieldwork revealed a number of heretofore unreported localities for the species, but did not extend the distributional limits beyond those previously reported in the literature (Zimmer, 1938a; Bond, 1947; Meyer de Schauensee, 1966). Since the preferred habitat extends for some distance northward into southwestern Ecuador, it is likely that this species will eventually be found there also, though I failed to find it during the eight days that I searched suitable habitat in extreme southwestern Ecuador in 1976.

Specimens examined, 43; localities, from north to south (see fig. 71; asterisks denote author's study areas): PERU, Tumbes, Tumbes;

TABLE 46
Measurements (in Millimeters and Grams) in Samples of *Myiarchus semirufus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	17	85 - 91	88.5 $\pm$ 0.48	1.97	2.23
Females	9	82 - 87	84.9 $\pm$ 0.56	1.69	1.99
Tail Length					
Males	16	82 - 88	85.0 $\pm$ 0.50	2.00	2.35
Females	9	78 - 84	81.4 $\pm$ 0.71	2.13	2.61
Body Weight					
Males	4	21.7 - 24.0	22.7 $\pm$ 0.52	1.04	4.60
Females	3	21.0 - 25.0	22.8 —	—	—

Talara, Piura; Sullana, Piura (Chilaco; Pílares; Somate); *San Lucas, Piura; *Jayanca, Lambayeque (Olmos); Chepén, La Libertad (Pacasmayo; Guadalupe; Tembladera, Cajamarca);

*Paiján, La Libertad (Trujillo; Cartavio; Virú); Hacienda de Suchiman, Ancash; *Casma, Ancash (Chimbote); Huarmey, Ancash; Paramonga, Lima (Huariconga).

MYIARCHUS TYRANNULUS (MÜLLER)

The Middle American populations of this wide-ranging Middle and South American species extend from central Costa Rica northward to the southwestern United States (Lanyon, 1960), and are separated from the South American populations by a distributional hiatus in southern Costa Rica and all of Panama. The species is found virtually throughout the arid and semi-arid tropical zone of South America, east of the Andes from northern Colombia to northern Argentina, but apparently now absent from much of the more mesic western and central parts of the Amazon basin (fig. 76). The species is polytypic, and two South American subspecies are recognized here, *tyrannulus* and *bahiae*, neither of which is considered to be migratory.

Populations in the Lesser Antilles (*nugator*, *sanctaeluciaae*, *oberi*, *sclateri*, and *berlepschii*) that have been assigned to *M. tyrannulus* by most authors have been shown not to belong with this species (Lanyon, 1967).

DIAGNOSIS: The only large South American *Myiarchus* (wing length greater than 80 mm.) with the inner vanes of the rectrices conspicuously marked (at least 3 mm. wide on one or more rectrices) with Antique Brown and with underparts characteristic of most *Myiarchus* (yellow abdomen and gray-white throat). In

fresh specimens, mandible variable; usually all black, but sometimes slightly paler basally; paling also occurs in older museum specimens. Color of mouth lining pale Orange Yellow.

Vocal response to intruding conspecifics consists of repeated "hui" notes, slowly modulated whistles (vibrato), and rasps that typically involve a pronounced deviation from the carrier frequency. Dawn song consists of isolated "hui" notes alternated with more complex phrases in which the rapid "hui" notes reveal a prominent glissando in the ascending segment of each component.

HABITAT (FIGS. 22-23, 27-28, 64, 77-78, 80): Tropical and lower subtropical zones. Borders of woodlands, wooded areas along rivers and streams, wooded savannas, xerophytic scrub; habitats tend to be more arid than mesic.

The species appears to be more responsive to the arid character of the environment than to elevation *per se*, and is frequently found above 900 m. in Bolivia, with specimens taken as high as 1700 m. I found it as high as 1200 m. in Peru. In view of the species' preference for the more arid habitats in general, it is curious that some populations are confined mainly to mangroves, as in Trinidad, Tobago, and Surinam.

BREEDING AND ANNUAL CYCLE: The spe-

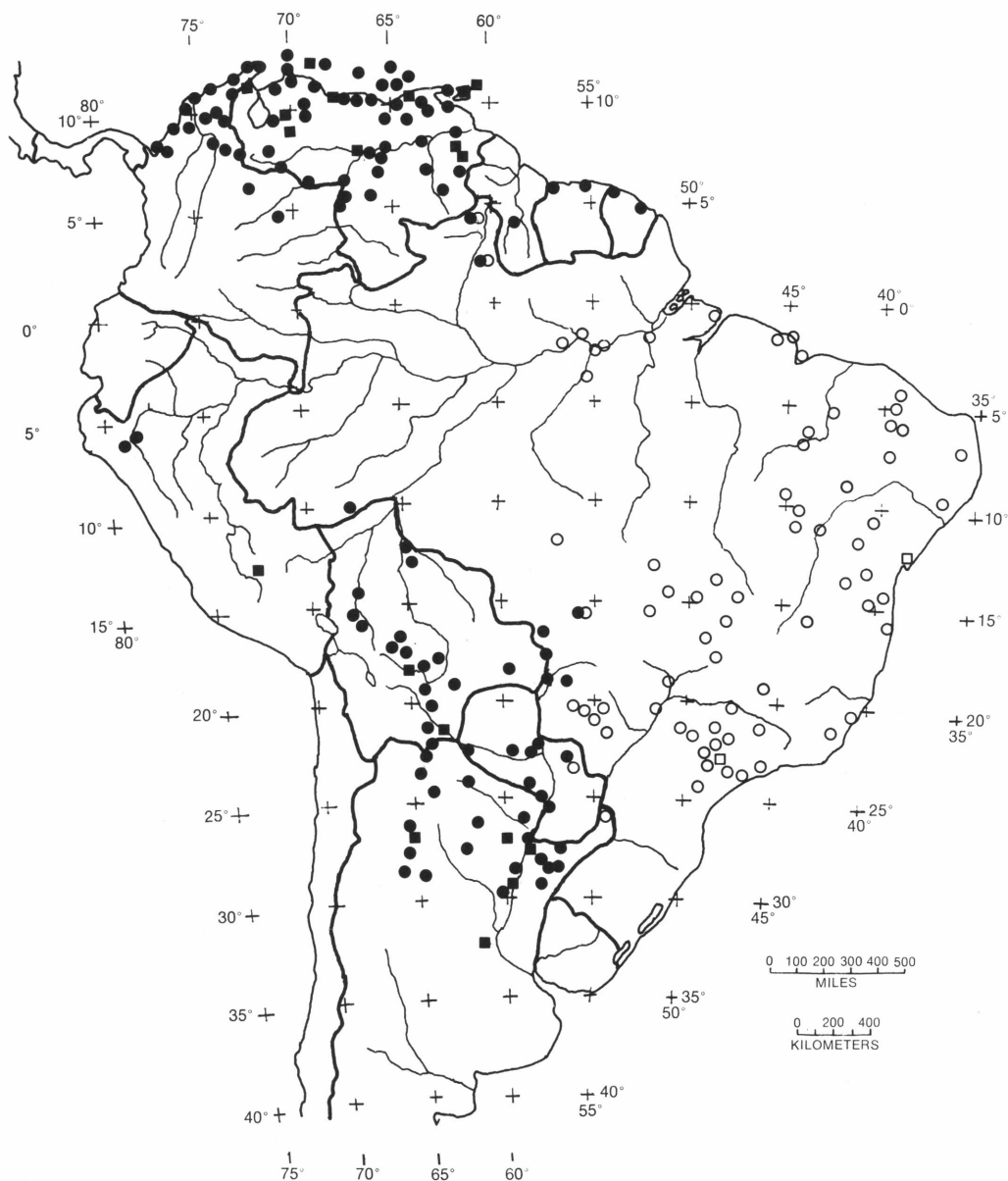


FIG. 76. Distribution of *Myiarchus tyrannulus tyrannulus* (solid symbols) and of *M. t. bahiae* (open symbols) as indicated by localities of specimens examined (circles) and by sites where author studied this species in the field (squares). See pages 598 and 602 for a list of these localities and page 594 for an itinerary of author's fieldwork with this species.

cies is a cavity nester and uses nesting materials similar to those of other members of the genus. Two nests were discovered during this study. On November 17, 1967, George Powell,

prompted by the behavior of a pair of *M. t. tyrannulus* with which we had been conducting playback experiments, investigated a natural cavity (fig. 79) about 7.5 m. above the ground



FIG. 77. Habitat of *Myiarchus tyrannulus tyrannulus*. *Top*: Tropical xerophytic community on the island of Curaçao, Dutch West Indies, April 1968; elevation near sea level. *Bottom*: A lime-coconut plantation near Roxborough, on the island of Tobago, May 1968; elevation near sea level.

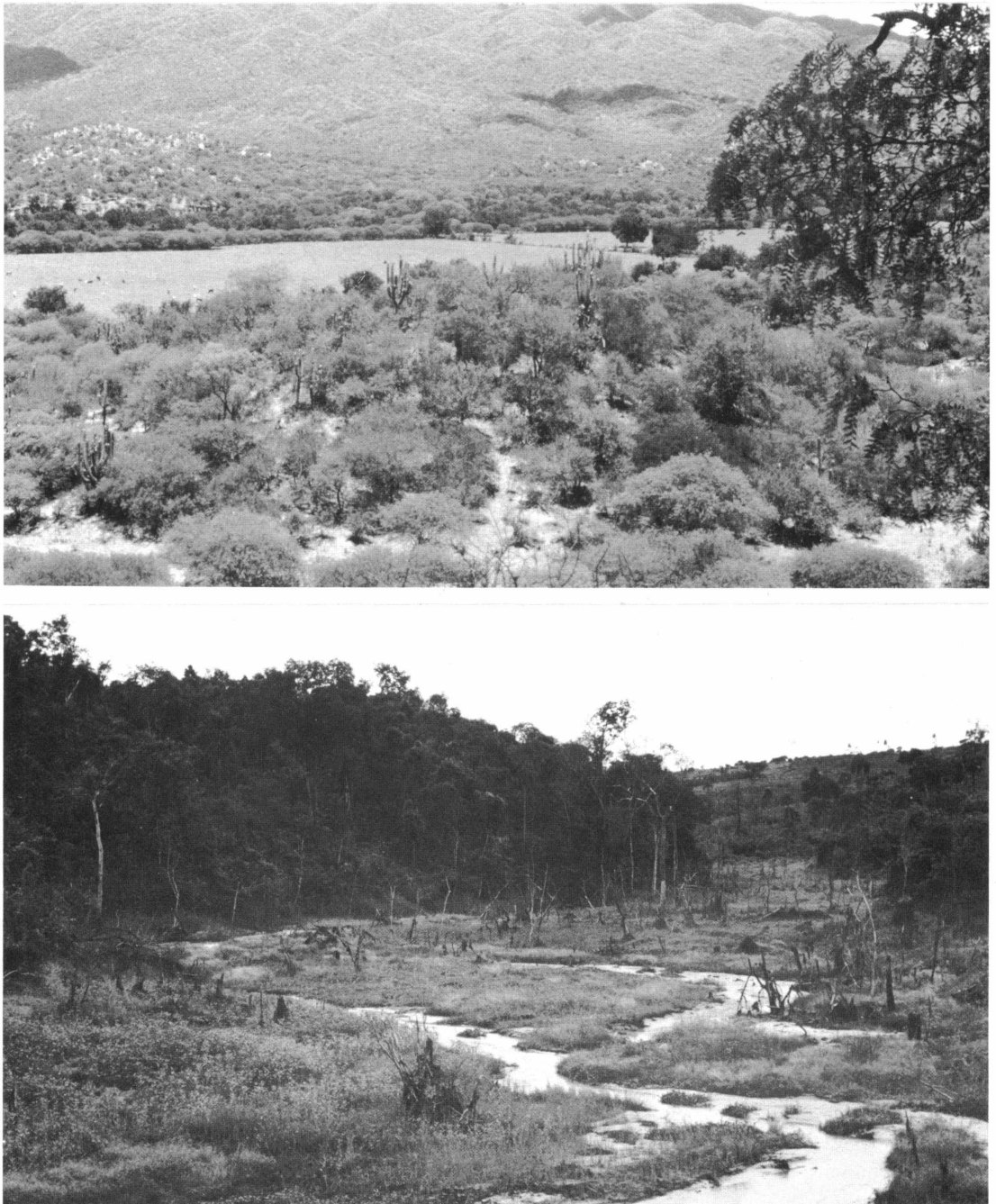


FIG. 78. *Top*: Habitat of *Myiarchus tyrannulus tyrannulus* in subtropical, xerophytic woodland near Tucumán, Argentina, November 1967; elevation 500 m. Sympatric with *M. swainsoni ferocior* at this locality. *Bottom*: Habitat of *M. tyrannulus bahiae* near the Rio Tiete, Anhembi, Department of São Paulo, Brazil, December 1967; elevation 500 m. Sympatric with *M. ferox australis* and *M. s. swainsoni* at this locality.

in a live mesquite (*Prosopis* sp.) near San Miguel de Tucumán, Argentina. The cavity contained a nest of small twigs, lined with shed snakeskin and hair presumably plucked from a dead opossum (*Didelphis* sp.) (fig. 79). The clutch of five eggs included three *tyrannulus* eggs and two eggs of the Shiny Cowbird, *Molothrus bonariensis*, a brood parasite. Nests of *M. crinitus* are rarely parasitized by the Brown-

headed Cowbird, *Molothrus ater*, presumably because of its hole-nesting habits (Friedmann, 1963; Friedmann, Kiff, and Rothstein, 1977), and this record may be the second of *M. tyrannulus* being parasitized by *bonariensis* (Friedmann, Kiff, and Rothstein, 1977). A second nest was found by David Ewert at our study area near Villa Lola, Bolívar, Venezuela, on May 1, 1970 (fig. 80). The cavity, which was



FIG. 79. Nest cavity (left) of *Myiarchus tyrannulus tyrannulus* located about 7.5 m. off the ground in a live mesquite tree near Tucumán, Argentina, November 1967; elevation 500 m. Nest (right) was constructed of small twigs and lined with shed snakeskin and hair.

open at the top, was in a wooden fence post, about 1.5 m. above the ground, and contained bits of shed snakeskin and lizard skin, as well as hair (apparently from cows). There were three *tyrannulus* eggs in the nest when it was first discovered and again on the following day when the incubating female was flushed from the cavity. The eggs in both the Argentine and Venezuelan clutches were indistinguishable from those of *M. crinitus* in size, color, or markings.

There are numerous observations in the literature confirming that *M. tyrannulus* is a cavity nester, that the nest typically contains hair, feathers, and shed snakeskin, and that the eggs are not distinguishable from those of *M. crinitus* (Dalglish, 1889; Robinson and Richmond, 1895; Allen, 1905; Hartert and Venturi, 1909; Ihering, 1914; Cherrie, 1916; Belcher and Smooker, 1937; Herklots, 1961). Clutch size in these references varies from two to four, with three being the most frequently cited number of eggs.

Breeding records for the northern population of *M. t. tyrannulus* extend from April through July. The earliest egg date known to me is April 8, in Bolívar, Venezuela (Cherrie, 1916), and Santa Marta, Colombia (Allen, 1905), and the latest is July 10 on Margarita Island, Venezuela (Robinson and Richmond, 1895).

The southern population of *M. t. tyrannulus* and also *M. t. bahiae* breed from October through December. Males taken in northeastern Argentina in late October had fully enlarged testes, measuring 11 to 14 mm. by 4 to 7 mm., but the earliest egg date known to me is November 7, in Paraguay (Dalglish, 1889).

The definitive plumage is renewed during a complete, prebasic molt that follows breeding. In the northern population of *M. t. tyrannulus*, specimens showing active molt of the remiges have been taken from July through December. Since the molt of the remiges is well advanced in some of the July specimens, the period of active molt probably begins as early as June in some individuals. A very worn specimen that I took in western Venezuela on May 14 showed some body molt. In the southern population of *M. t. tyrannulus*, and in *M. t. bahiae*, specimens showing active molt of the remiges have been taken from December through May.

Olrog (1963) stated that the Argentine population of *tyrannulus* migrates to the Guianas, Venezuela, and Colombia during the austral winter. Since individuals from the southern population of *tyrannulus* are not distinguishable from resident northern birds, evidence for migratory behavior in the southern population has to be based on the absence of *tyrannulus* during the austral winter. I have seen 42 specimens of *tyrannulus* (AMNH, MACN, MCZ, IML, and MLP) taken in Argentina during the winter months of May (21 specimens), June (11 specimens), July (six specimens), and August (four specimens). This does not refute the possibility that some Argentine individuals may leave their breeding range during the winter, but does demonstrate that some of the population is resident. Zimmer (1938a) believed the species to be nonmigratory.

VOCAL CHARACTERS: The analysis of vocal characters of *M. tyrannulus* is based on recordings from these samples:

M. t. tyrannulus—Curaçao, three pairs;



FIG. 80. David Ewert inspects a top opening nest cavity of *Myiarchus tyrannulus tyrannulus* near Villa Lola, Bolívar, Venezuela, on May 1, 1970; elevation 300 m. Nest contained a full clutch of three eggs.

Trinidad, one pair; Tobago, three pairs; Venezuela, 11 pairs; Peru, one pair; Bolivia, four pairs; Argentina, six pairs

M. t. bahiae—Brazil: Bahia, two pairs; São Paulo, two pairs

CALLS: The vocal repertoire of this species,

as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 81-84.

In response to playback, or when excited by intruding conspecifics, *M. tyrannulus* vocalizes with series of "huit" notes, rasps, slowly mod-

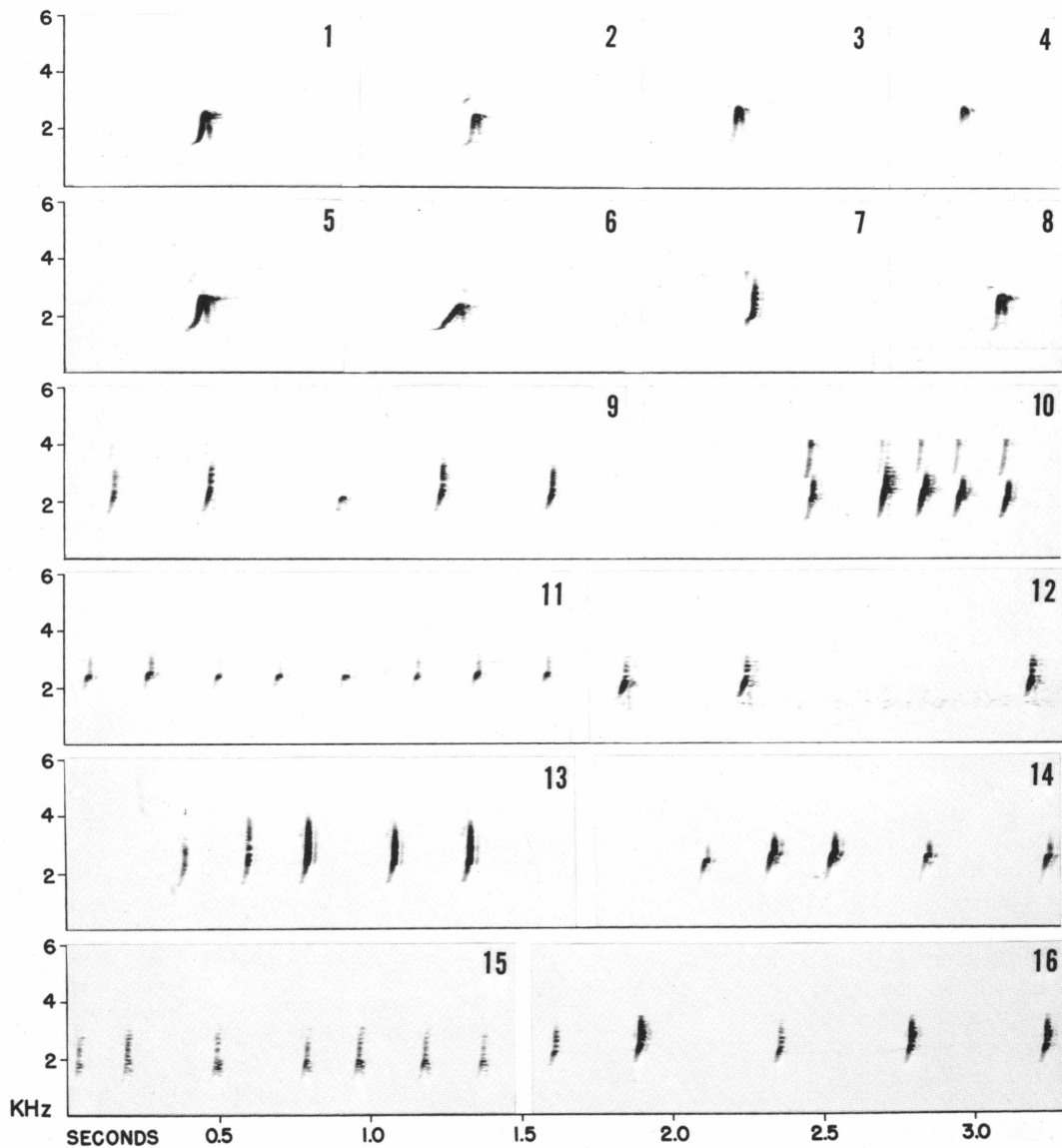


FIG. 81. Variation in vocal characters of *Myiarchus tyrannulus*: "huit" notes. These spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. tyrannulus* (Curaçao, 5, 9; Tobago, 8; Venezuela, 6, 7, 10, 11; Bolivia, 1, 12; Argentina, 2, 13, 14); *M. t. bahiae* (Brazil, 3, 4, 15, 16).

ulated whistles (vibrato), and rapid "huit" notes. The most conspicuous and frequently delivered call in the repertoire of *M. tyrannulus* is the "huit," the actual configuration of which can be quite variable (fig. 81). Normally, the call is a simple, chevron-like note, rendered at infrequent intervals (fig. 81:1-8). When highly stimulated as in response to playback, individuals may deliver a series of "huit" notes at the rate of 3 to 6 per second (fig. 81:9-16). The notes in a series of this kind tend to consist of the glissando that represents the ascending portion of the chevron, and average greater amplitude. When the rendition of "huit"-like notes reaches a rate of 10 to 20 per second, as it sometimes does, I have labeled the resulting phrase the rapid "huit" call (fig. 83:9-15). The rasp (fig. 82:14-28) may be given in a series or as an isolated call, and exhibits a variable deviation from the carrier frequency, presumably attributable to different levels of motivation. Another call often interjected into the vocal response to playback is a slowly modulated whistle or vibrato (fig. 82:1-13), less than 0.3 second in length in my sample. The carrier frequency of this note rises perceptibly and is modulated at a moderate frequency of 20 to 30 Hz. The energy in this whistled note normally is continuous throughout, rather than being pulsed.

Foraging birds not excited by playback or intruding conspecifics deliver isolated "huit" notes at irregular intervals. Another call given under similar circumstances is one that I have labeled the "whay-burg" call (fig. 83:1-8), and which consists of two parts: an introductory syllable, derived from a single "huit" note (with considerable frequency excursion), followed quickly by a phrase made up of two or three "huit" notes given in rapid succession. The introductory syllable is accented, and the two parts of the call are rendered so quickly as to suggest a bi-syllabic call to the human ear, even though the second part includes two or three notes. Presumably, these isolated "huit" notes and "whay-burg" notes serve as location calls between members of a pair. I have elicited these calls from birds whose mates had recently been collected.

DAWN SONG: The dawn song of the male

M. tyrannulus consists of alternated renditions of isolated "huit" notes and complex phrases that are typically derived from the combination of a "whay-burg" note with a brief series of rapid "huit" notes (fig. 84). A variation of this complex phrase is effected by a slow modulation of the introductory "huit" component of the "whay-burg" note, thus producing a trace somewhat similar to that of the vibrato or slowly modulated whistle given during daylight. The isolated "huit" syllables are a consistent and conspicuous component in the dawn song of this species.

GEOGRAPHICAL VARIATION: I have no evidence in my samples to suggest that there is geographical variation in any of the vocal characters of *M. tyrannulus*.

ITINERARY OF FIELDWORK

- 1963—March 9-11, with *tyrannulus* on Trinidad, West Indies.
- 1967—November 2-19, with *tyrannulus* near Tucumán, Tucumán, Argentina; November 29 through December 4, with *bahiae* at Fazenda Barreiro Rico, near Anhembi, São Paulo, Brazil; December 20-21, with *bahiae* near Salvador, Bafa, Brazil.
- 1968—April 22-24, with *tyrannulus* on Curaçao, Netherlands Antilles; April 27 through May 1, with *tyrannulus* near Ocumare de la Costa, Aragua, Venezuela; May 12-14, with *tyrannulus* near Barinas, Barinas, Venezuela; May 17-18, with *tyrannulus* near San Fernando de Apure, Apure, Venezuela; May 20-22, with *tyrannulus* near Upata, Bolívar, Venezuela; May 24-29, with *tyrannulus* on Tobago, West Indies.
- 1969—May 9-16, with *tyrannulus* near San Fernando de Apure again (and neighboring Guárico, Venezuela); May 21-23, with *tyrannulus* near Barinas again.
- 1970—April 30 through May 6, with *tyrannulus* in northeastern Bolívar, Venezuela (Villa Lola; Guasipati; El Callao; El Palmar; El Manteco); May 9-10, with *tyrannulus* near Cumaná, Sucre, Venezuela; May 14-15, with *tyrannulus* near Cerro El Cedro, Zulia, Venezuela; November 8, with *tyrannulus* near Reconquista, Santa Fé, Argentina; November 9-22, with *tyrannulus* at Las Tres Marías, Corrientes, Argentina; November 23, with *tyrannulus* in southeastern Chaco, Argentina.

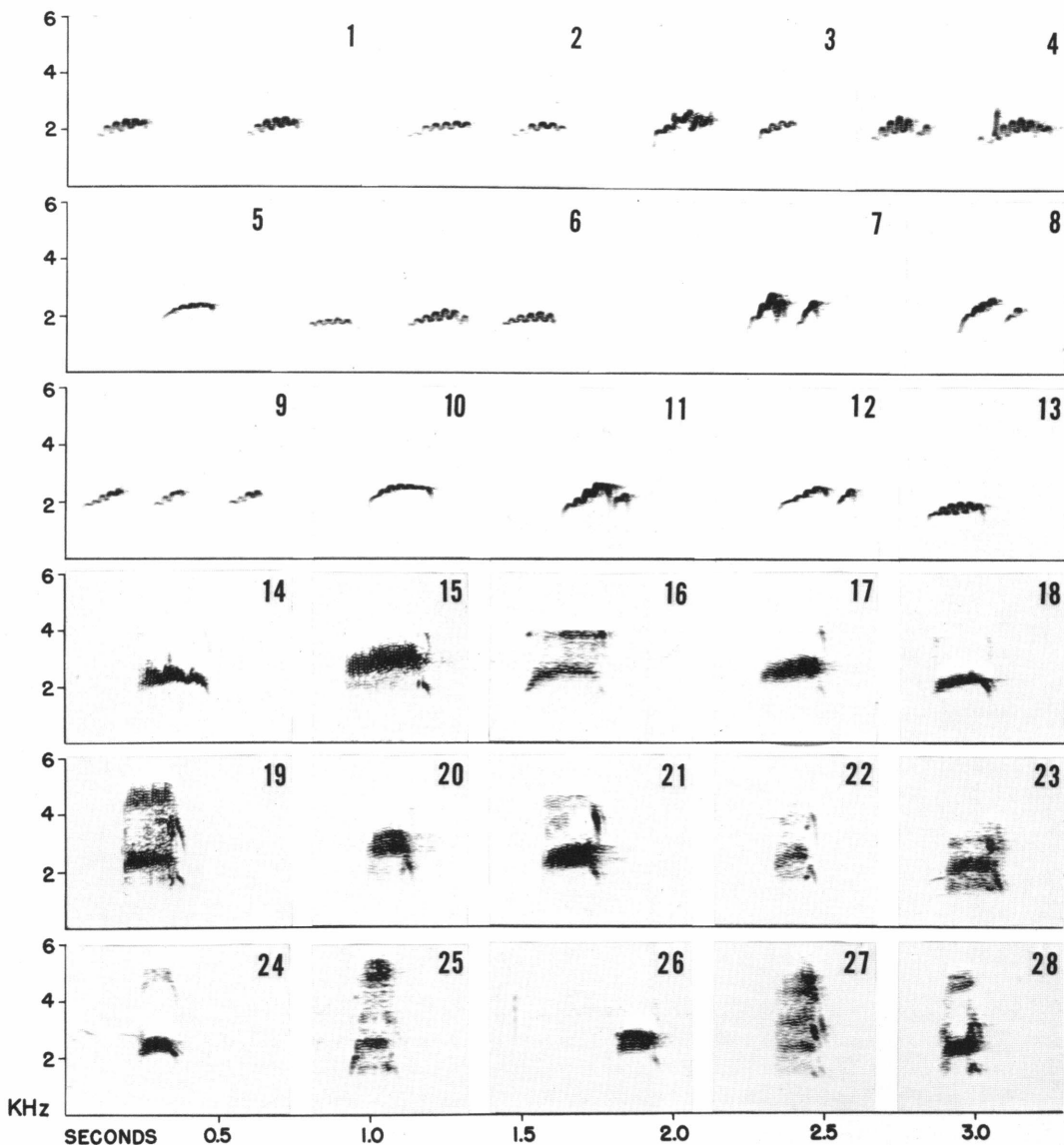


FIG. 82. Variation in vocal characters of *Myiarchus tyrannulus*: slowly modulated whistles (vibrato) (1-13) and rasps (14-28). These spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. tyrannulus* (Curaçao, 1, 14, 15; Trinidad, 2; Tobago, 16; Venezuela, 3-7, 17-21; Bolivia, 22; Argentina, 8-11, 23-25); *M. t. bahiae* (Brazil, 12, 13, 26-28).

(Machagai; La Escondida; Resistencia); November 28-29, with *tyrannulus* near Tucumán again; December 3, with *tyrannulus* near Angélica, Santa Fé, Argentina; Decem-

ber 10-14, with *bahiae* at Fazenda Barreiro Rico again.
1972—November 20-21, with *tyrannulus* near Quillabamba, Cuzco, Peru.

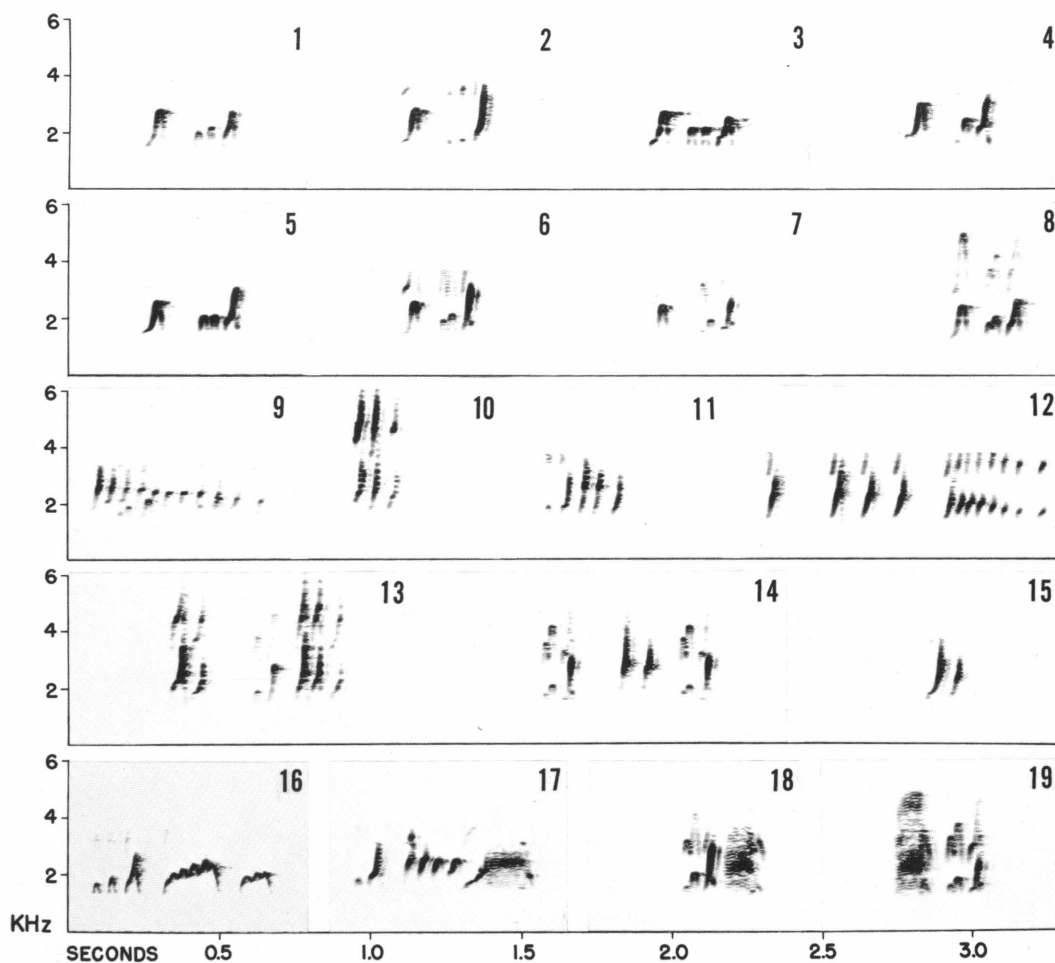


FIG. 83. Variation in vocal characters of *Myiarchus tyrannulus*: "whay-burg" notes (1-8), rapid "huit" notes (8-15), and combinations of calls (16-19). Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. tyrannulus* (Curaçao, 1, 9, 10, 16; Venezuela, 2, 3, 11, 12, 17; Bolivia, 4, 5; Argentina, 6, 13, 18); *M. t. bahiae* (Brazil, 7, 8, 14, 15, 19).

1974—May 3, with *tyrannulus* near Pie de Cuesta, Lara, Venezuela; November 5-7, with *tyrannulus* near Villa Montes, Tarija, Bolivia; November 12, with *tyrannulus* near Puente Arce, Chuquisaca, Bolivia.

SYSTEMATICS

Myiarchus tyrannulus tyrannulus (Müller)

Muscicapa tyrannulus Müller, 1776, p. 169 (type locality, Cayenne, French Guiana; based on Daubenton, 1765-1780, No. 571, fig. 1).

Muscicapa aurora Boddaert, 1783, p. 34 (type lo-

cality, Cayenne, French Guiana; based on Daubenton, *loc. cit.*).

Myiarchus erythrocerus Scater and Salvin, 1868, p. 628 (type locality, Caracas, Venezuela).

Myiarchus tyrannulus: Scater, 1888, p. 251 (new combination).

Myiarchus tyrannulus cholorepiscus Berlepsch and Leverkühn, 1890, p. 16 (type locality, Cuyabá, Mato Grosso, Brazil; cotypes in Kiel Museum). Berlepsch, 1907, p. 476. Hellmayr, 1927, p. 164 (synonymy).

Myiarchus brevipennis Hartert, 1892, p. 12 (type locality, Savonet, Curaçao, Dutch West Indies;

holotype in the American Museum of Natural History, examined).

Myiarchus tyrannulus brevipennis: Hellmayr, 1906, p. 26 (new combination). Berlepsch, 1907, p. 476. Hellmayr, 1927, p. 163 (synonymy). Phelps and Phelps, 1963, p. 187. Zimmer, MS.

Myiarchus tyrannulus tyrannulus: Clark, 1905, p. 276. Berlepsch, 1907, p. 476. Todd, 1922, p. 185 (synonymy). Hellmayr, 1927, p. 163 (in part; synonymy). Zimmer, 1938a, p. 1.

Myiarchus tyrannulus tobagensis Hellmayr and Seilern, 1914, p. 89 (type locality, Man-of-War

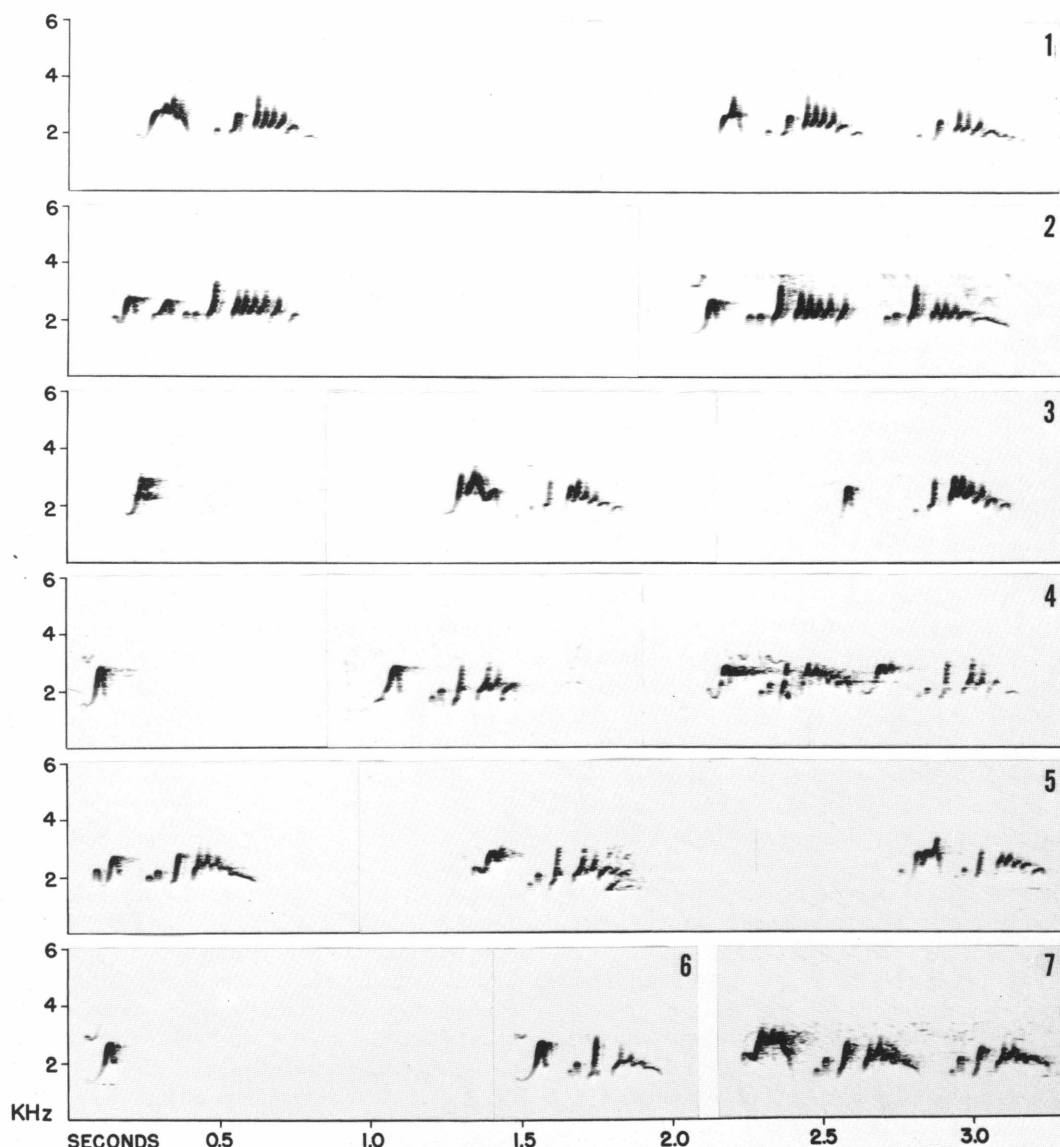


FIG. 84. Variation in vocal characters of *Myiarchus tyrannulus*: dawn song. Spectrograms were made with 45 Hz. filter and are from recordings of the following populations: *M. t. tyrannulus* (Curaçao, 1; Tobago, 2; Venezuela, 3; Bolivia, 4, 5; Argentina, 6, 7).

Bay, Tobago; holotype in the Munich Museum). Hellmayr, 1927, p. 166. Zimmer, MS.

Myiarchus tyrannulus blaquilla Phelps, 1947, p. 103 (type locality, Isla La Blanquilla, Venezuela; holotype in the Phelps Collection, on deposit in the American Museum of Natural History, examined). Zimmer, MS. Phelps and Phelps, 1963, p. 188.

DIAGNOSIS: Separable from *bahiae* by having a well-defined stripe of Fuscous extending along the rachis in the outer vane of the outer rectrix, averaging 4 mm. wide but varying in width from 2 to 7 mm. Typically, this dark stripe is of nearly equal width throughout its length and has a sharply defined outer border; more rarely, it becomes diffuse, with the Fuscous extending in an irregular and poorly defined pattern toward the outer edge of the outer vane, thus approaching the condition in *bahiae*.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 76): In addition to insular populations off northern South America, there are two apparently disjunct populations on the South American continent. In the north the form is known from the Dutch West Indies (Aruba, Curaçao, and Bonaire), Isla La Blanquilla, Trinidad, Tobago, northern Colombia, Venezuela (except southern Amazonas and Bolívar), and northern Guyana, Surinam, and French Guiana. South of an apparent distributional hiatus in southern Colombia, Ecuador, and western Brazil, the form is known from northern and eastern Peru, Bolivia, Paraguay, and northern Argentina. Intergrades with *bahiae* in Mato Grosso and Rio Branco in Brazil, Paraguay, and northeastern Argentina.

The northern population of *tyrannulus* is sympatric with *M. panamensis* west of the Andes, with *M. ferox* east of the Andes, and with *M. venezuelensis* locally across northern Colombia and Venezuela, and Tobago. In ecological habitats *tyrannulus* may occur with *M. tuberculifer*.

The southern population of *tyrannulus* is sympatric with *M. ferox* and *M. swainsoni* virtually throughout its range, and with *M. tuberculifer* along the western perimeter of the Amazon basin.

Specimens examined, 748; localities, by country, from north to south and west to east

(see fig. 76; asterisks denote author's study areas): NETHERLANDS ANTILLES, Aruba; *Curaçao; Bonaire. VENEZUELA, Moruy, Falcón; Islas Los Roques; Isla La Blanquilla; Islas Los Testigos; San Luis, Falcón; *Cerro El Cedro, Zulía (Maicao, and Carraipía, in Guajira, Colombia); Dabajuro, Falcón (Casigua); Mirimire, Falcón (Boca del Río Tocuyo); Tucacas; San Juan de los Cayos; Isla La Tortuga; Isla de Margarita (Islas Los Frailes); Cristóbal Colón, Sucre (Isla Patos; Guiría); *Ocumare de la Costa, Aragua (Maracay; Puerto Cabello, Carabobo); El Limón, Aragua; Santa Lucía, Miranda; Tacarigua, Miranda; *Cumaná, Sucre (Cumanacoa; Carúpano; Los Altos; Los Palmales; Cocollar); San Antonio, Monagas; El Cují, Lara; Barcelona, Anzoátegui (Píritu; Bergantín); Maturín, Monagas Pederuales, Delta Amacuro (Capure); Sabana de Mendoza, Trujillo; *Pie de Cuesta, Lara; Acarigua, Portuguesa; Zaraza, Guárico; Cantaura, Anzoátegui; *Barinas, Barinas; Los Castillos, Delta Amacuro; Ciudad Bolívar, Bolívar (Candelarita; Soledad, Anzoátegui); Santa Bárbara, Barinas; *San Fernando de Apure, Apure (and neighboring Guárico); Caicara, Bolívar (Santa Rita, Guárico); Altigracia, Bolívar (Río Suata, and Barrancas, in Anzoátegui); *Upata, Bolívar (El Palmar; Villa Lola); Santa Rosalía, Bolívar (El Cambur; Maripa; Río Cuchivero; Río Guaniamo); *El Callao, Bolívar (El Manteco; Guasipati; Tumeremo); El Amparo, Apure (Guasqualito); Raudal Alto, Bolívar; La Paragua, Bolívar; El Dorado, Bolívar; Alto Río Meta, Apure (Cararabo); Puerto Páez, Apure; Caño Cataniapo, Amazonas (Puerto Ayacucho); El Platanal, Amazonas; Cerro Auyan-tepui, Bolívar; Maipures, Amazonas. COLOMBIA, Bahía Partete, Guajira; Nazaret, Guajira; Riohacha, Guajira; Santa Marta, Magdalena (Camperucho; Mamatoco); Conejo, Guajira; Barranquilla, Atlántico; Turbaco, Bolívar (Aguada de Pablo, and Los Pendales, in Atlántico); Caracolicito, Magdalena (El Difícil); "Camp Costa Rica," Magdalena; Casacará, Cesar; Coveñas, Sucre; Colosó, Sucre; Norosí, Bolívar; Nicoclí, Antioquia; Quimarí, Córdoba (Nazaret; Río Sinú); Pueblo Nuevo, Norte de Santander; Cúcuta, Norte de Santander; Palmar, Boyacá; Carimagua, Meta. *TRINIDAD (and Monas). *TOBAGO.

TABLE 47
Measurements (in Millimeters and Grams) in Samples of *Myiarchus tyrannulus*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
<i>M. t. tyrannulus</i>					
(northern population)					
Wing Length					
Males	94	87 - 99	93.9 ± 0.27	2.63	2.80
Females	79	85 - 95	89.4 ± 0.25	2.20	2.46
Tail Length					
Males	97	78 - 95	86.2 ± 0.30	2.96	3.43
Females	78	76 - 87	82.1 ± 0.28	2.45	2.98
Body Weight					
Males	3	28.3 - 29.8	29.2 —	—	—
Females	4	27.1 - 32.5	29.4 —	—	—
<i>M. t. tyrannulus</i>					
(southern population)					
Wing Length					
Males	139	90 - 102	97.0 ± 0.19	2.28	2.35
Females	85	89 - 99	93.4 ± 0.23	2.09	2.24
Tail Length					
Males	145	80 - 93	88.2 ± 0.22	2.63	2.98
Females	91	77 - 89	84.6 ± 0.25	2.35	2.77
Body Weight					
Males	4	27.0 - 30.4	28.3 —	—	—
Females	5	22.2 - 30.0	28.0 —	—	—
<i>M. t. bahiae</i>					
Wing Length					
Males	107	90 - 100	95.2 ± 0.22	2.22	2.34
Females	65	86 - 96	91.1 ± 0.26	2.12	2.33
Tail Length					
Males	115	80 - 94	86.5 ± 0.25	2.70	3.12
Females	69	79 - 87	82.4 ± 0.25	2.10	2.54
Body Weight					
Males	2	28.0 - 32.0	30.0 —	—	—
Females	2	23.9 - 31.0	27.5 —	—	—

GUYANA, Annai. SURINAM, Nickerie; Paramaribo. FRENCH GUIANA, Mana; Cayenne. PERU, Jaén, Cajamarca (Bellavista; Bagua Chica, Amazonas); Pucará, Cajamarca; *Quillabamba, Cuzco (Santa Ana; Urubamba Valley). BRAZIL, Plácido de Castro, Acre; Descavaldos, Mato Grosso; Corumbá, Mato Grosso (Urucum; Puerto Suarez, Santa Cruz, Bolivia); Palmiras, Mato Grosso. BOLIVIA, Río Iténez, El Beni; San Joaquín, El Beni; Chatarona, El Beni; Guanay, La Paz; Santa Ana, La Paz; Todos Santos, Cochabamba; Incachaca, Cochabamba (Palmar); Pojo, Cochabamba; Buena Vista, Santa Cruz (Río Surutú; Vermejo; Nueva Moka; San Carlos; Cercado); Lago Gaiba Mirim, Santa Cruz;

Chilón, Santa Cruz (Comarapa; Ele-Ele, Cochabamba); *Puente Arce, Chuquisaca (Río Grande); Cerro San Micerato, Santa Cruz; Parapeti, Santa Cruz; Río Azuero, Chuquisaca; Monteagudo, Chuquisaca (Gutiérrez, Santa Cruz); Entre Ríos, Tarija; *Villa Montes, Tarija; Yacuiba, Tarija (Aguaray, Salta, Argentina). PARAGUAY, Puerto Casado, Chaco; Guachalla, Chaco; Orloff, Chaco (Lichtenau; Fort Wheeler); 25 km. and 80 km. W of Puerto Pinasco, Chaco; Zanja Moroti, Yhu; Río Negro, Chaco; Trinidad, Chaco; Nueva Italia, Paraguari. ARGENTINA, Urundel, Salta (Orán; Embarcación; Miraflores; Yuto, Jujuy; Río Bermejo, and Río Lipeo, in Tarija, Bolivia); Santa María, Salta; Ingeniero Juárez,

Formosa; Río del Valle, Salta; San Pedro de Colalao, Tucumán (Trancas); Pampa de los Guanacos, Santiago del Estero; Pirané, Formosa; *Tucumán, Tucumán (Tafi Viejo; Tapia); *Sáenz Peña, Chaco (Machagai; La Escondida); Las Palmas, Chaco; Concepción, Tucumán (La Cocha; Monteagudo; Leales); Girardet, Santiago del Estero; *Las Tres Marías, Corrientes (Corrientes; Itatí; San Luis del Palmar; Empedrado; Resistencia, Chaco); Ituzaingó, Corrientes; Manantiales, Corrientes; Pomancillo, Catamarca; Choya, Santiago del Estero; Ocampo, Santa Fé (Mocovi); Concepción, Corrientes; Carlos Pellegrini, Corrientes; *Reconquista, Santa Fé; Mercedes, Corrientes; La Guampita, Santa Fé; *Angelica, Santa Fé.

RELATIONSHIP OF

Myiarchus tyrannulus AND *Myiarchus nugator*

I have recommended (Lanyon, 1967) that *M. nugator* of the southern Lesser Antilles be considered a monotypic species endemic to the Windward Islands. I further argued that it should be treated as a member of the super-species *tyrannulus*, to indicate its close relationship to this wide-ranging South and Middle American species. Though barely differentiated morphologically and vocally from the continental species, most pairs of *nugator* tested with experimental playback were able to discriminate between their own vocal repertoire and that of *M. tyrannulus*, and failed to respond to a tape of the latter.

One objective of the later work with *M. tyrannulus* in South America was to conduct the reciprocal test, to determine the response of populations of that form to playback of *M. nugator*. Playback experiments using, in part, a standardized tape of *M. nugator* were run with territorial *M. t. tyrannulus* in northern and eastern Venezuela, Tobago, Curaçao, and in northwestern and northeastern Argentina, and with *M. t. bahiae* in southern Brazil. In all instances the birds failed to respond positively to the playback of *M. nugator* tape, thus confirming the conclusion from the earlier West Indian study. A series of experiments with a territorial pair of *M. t. tyrannulus* near Tucumán, Argentina, on November 10, 1967, illustrates this discriminatory ability:

Experiment 6—study area two. Tapes used, Argentine *tyrannulus* vs. *M. nugator*. Birds calling just outside experimental area at start at 8:48 A.M. Within 30 seconds, one bird made a pass at the *tyrannulus* model. In a study 4 ft. from model, calling well. Mate showed at 8:50, 30 ft. from model. Crisscrossing; one bird 12 ft. from *tyrannulus* model, calling. A third *tyrannulus* briefly moved through the area, causing interaction. At 8:53, one bird perched 20 ft. behind *tyrannulus* model. No response to *nugator*. Both birds crisscrossed at 8:55. Another crisscross. Some interaction between them. Cable switch at 8:55. Both birds reoriented within 30 seconds. One almost hit new *tyrannulus* model at 8:56. Calling well 15 ft. from new *tyrannulus* model. No response at all to *nugator*. In a study at 15 ft., calling well, at 8:59. Both birds crisscrossing *tyrannulus* model. Crisscross again. Pass at *tyrannulus* model at 9:00. Pass within 3 ft. of model at 9:01. Second bird in a similar pass. Study at 15 ft., calling well; remained there until end of experiment.

Experiment 7—same locality, pair, and date as above. Tapes used, *M. swainsoni ferocior* vs. *M. tuberculifer*. Birds calling in general area at start at 9:06 A.M. No response from pair of *tyrannulus*. A *ferocior* showed in *ferocior* area and went into a study about 10 ft. from the model, calling quietly. Good strong response from *ferocior* to *ferocior* model, including reorientation at cable switch, but no response at all from *tyrannulus* to these two neutral tapes.

Experiment 8—same locality, pair, and date as above. Tapes used, *M. nugator* vs. *M. oberi sclateri*. Pair of *tyrannulus* now silent, location unknown. A *ferocior* calling quietly just outside experimental area. Start at 9:24 A.M. No response at all until 9:28, when a *tyrannulus* called from edge of experimental area. A *tyrannulus* called 20 ft. above *sclateri* model at 9:30, then left the area. Cable switch at 9:32. A *tyrannulus* perched 25 ft. above new *nugator* model at 9:34, but left immediately. No further response during remainder of this experiment.

Experiment 9—same locality, pair, and date as above. Tapes used, Venezuelan *tyrannulus* vs. *M. swainsoni ferocior*. Birds silent, location unknown at start at 9:42 A.M. A *tyrannulus* showed within 30 seconds, calling at edge of experimental area. Crisscrossed *tyrannulus* model at 9:43. Another crisscross. A *ferocior* showed at *ferocior* model at 9:45; in a study at 20 ft., then made a pass at *ferocior* model. The *tyrannulus* is 10 ft. from *tyrannulus* model, in a study; calling 20 ft. above model. The *ferocior* is still in a study 10 ft. from *ferocior* model at 9:47. The *tyrannulus* crisscrossed *tyran-*

nulus model. The *ferocior* made a pass at *ferocior* model at 9:47:30. The *tyrannulus* calling well, 15 ft. from *tyrannulus* model. The *ferocior* made a pass at *ferocior* model at 9:48. Both *tyrannulus* within 10 ft. of *tyrannulus* model. The *ferocior* is less than 10 ft. from *ferocior* model at cable switch at 9:49. The *ferocior* had reoriented to 25 ft. of new *ferocior* model within 30 seconds, then moved in to 15 ft. Good reorientation by both *tyrannulus*, to within 20 ft. of new *tyrannulus* model by 9:51. The *tyrannulus* in a crisscross of new model. The *ferocior* 30 ft. from *ferocior* model, in a study at 9:55. The *tyrannulus* left the area in a territorial encounter, and did not return before end of experiment at 9:56. Strong response of *tyrannulus* to tape of Venezuelan *tyrannulus*.

In addition to illustrating the failure of *M. t. tyrannulus* to respond to a playback tape of *M. nugator*, this series of experiments also demonstrates the responsiveness of southern populations of *M. t. tyrannulus* to the playback of a tape made from recordings of northern populations of this subspecies.

That *M. tyrannulus bahiae* is likewise unresponsive to the playback of *M. nugator* is illustrated by the following field notes that describe a series of experiments with a pair of *bahiae* near Anhembi, São Paulo, Brazil, on December 3, 1967:

Experiment 61—territory along the Rio Piracicaba, Fazenda Barreiro Rico. Tapes used, *M. nugator* vs. *M. swainsoni ferocior*. Experimental area is within territories of a pair of *M. s. swainsoni* and of *M. t. bahiae*. All birds silent, location unknown at start at 5:12 P.M. Two *tyrannulus* appeared within *ferocior* area at 5:14. A third *tyrannulus* also appeared in *ferocior* area at 5:16. All three birds were within 10 ft. of *ferocior* model, interacting with one another, at cable switch at 5:19. They moved to midpoint during second half of experiment, vocalizing. No consistent, oriented response.

Experiment 62—same locality, pair, and date as above. Tapes used, *M. s. swainsoni* vs. *M. tuberculifer*. All birds silent, location unknown at start at 5:30 P.M. Strong response, including reorientation from pair of *swainsoni* to *swainsoni* model. No sign of pair of *bahiae*.

Experiment 63—same locality, pair, and date as above. Tapes used, *M. s. ferocior* vs. *M. o. oberi*. All birds silent, location unknown at start at 5:50 P.M. No sign of either *bahiae* or nominate *swainsoni*. Discontinued experiment at the cable switch.

Experiment 64—same locality, pair, and date as above. Tapes used, Venezuelan *tyrannulus* vs. Argentine *tyrannulus*. Birds silent, location unknown at start at 6:05 P.M. Heard a *tyrannulus* almost at once; it perched 20 ft. from Argentine *tyrannulus* model at 6:21. A second bird appeared at 6:22, 30 ft. from the same model. One moved in to 15 ft. from model. A second pair of *tyrannulus* appeared at the midpoint at 6:24, calling well. All four birds within 30 ft. of Argentine *tyrannulus* model at cable switch at 6:27. One still calling well at 15 ft. from new Venezuelan *tyrannulus* model at 6:29, and none of the four birds had reoriented to new Argentine *tyrannulus* model by 6:29. Two birds moved to midpoint by 6:30; one had reoriented to new Argentine *tyrannulus* model by 6:31, 6 ft. from model. Two birds in new Argentine *tyrannulus* area and two in new Venezuelan *tyrannulus* area at 6:32. One 6 ft. from Argentine *tyrannulus* model, and one at 10 ft. from Venezuelan *tyrannulus* at end of experiment.

Myiarchus tyrannulus bahiae Berlepsch and Leverkühn

Myiarchus bahiae Berlepsch and Leverkühn, 1890, p. 17 (type locality, Bahia; location of type unknown).

Myiarchus ferox: Pelzeln, 1868, p. 116 (in part; specimen in the Vienna Museum, examined by Hellmayr, 1926, p. 165).

Myiarchus tyrannulus bahiae: Ihering, 1907, p. 294 (new combination). Berlepsch, 1907, p. 476. Todd, 1922, p. 191 (synonymy). Hellmayr, 1927, p. 165 (synonymy). Zimmer, 1938a, p. 2 (in text).

Myiarchus tyrannulus pallescens Cory, 1916, p. 343 (type locality, Juá, Ceará, Brazil; holotype in the Field Museum of Natural History). Todd, 1922, p. 192. Hellmayr, 1927, p. 166.

DIAGNOSIS: Separable from *tyrannulus* by not having an area of Antique Brown in the outer vane of the outer rectrix, or, rarely, with only a very diffuse area of Antique Brown not sharply defined from the Fuscous.

DISTRIBUTION AND SPECIMENS EXAMINED (FIG. 76): This form occurs from the lower Amazon basin southward through eastern Brazil to São Paulo and in Misiones, Argentina. Intergrades with *tyrannulus* in Mato Grosso and Rio Branco, Brazil, Paraguay, and northeastern Argentina.

Sympatric with *M. ferox* and *M. swainsoni*, and to a lesser extent with *M. tuberculifer*.

Zimmer's (MS) extension of the range of *bahiae* to Paraná was based on Sztolcman's (1926) specimens taken along the Rio Paraná. Sztolcman described a new subspecies, *czakii*, based on four specimens that have Antique Brown in the rectrices reduced to narrow margins only. I have not seen these specimens, but the plumage description and the measurements given by Sztolcman match juvenal *M. s. swainsoni*, and I think it probable that they are *swainsoni* and not *tyrannulus*, an interpretation shared by Pinto (1944, p. 168). I know of no other records of *M. tyrannulus* in Paraná.

Specimens examined, 265; localities, by country, from north to south and west to east (see fig. 76; asterisks denote author's study areas): BRAZIL, Ilha de Marajó, Pará; Obidos, Pará; Rio Xingú, Pará; Turiaçu, Maranhão; Ilha do Mangunça, Maranhão; Faro, Pará; Monte Alegre, Pará; Santarém, Pará (Igarape Brabo; Boca do Rio Tapajós; Aramanai); São Luiz, Maranhão; Fordlandia, Pará; Baturité, Ceará; Therezina, Piauí (Flores, Maranhão; Quixadá, Ceará; Mosquito, Ceará; Tabocas, Maranhão (São João dos Patos); Iguatu, Ceará; Urussuhy, Piauí; Joazeiro, Ceará; Curemas, Paraíba; Arará, Piauí; Gilbués, Piauí; Palmeira dos Índios, Alagoas; Parnaguá, Piauí (Corrente); Santa Rita do Rio Preto, Baía; Buritirama, Baía (Barra do Rio Grande); Lamarão, Baía; Rio Aricá, Mato Grosso (Alto Tapajós); Morro do Chapéo, Baía; *Salvador, Baía (Santo Amaro); Serra do Roncador, Mato Grosso; Tamburi, Baía; Formoso, Goiás (Serra Dourada); Giguí, Baía (Sincorá); Dumba, Mato Grosso; Rio das Almas, Goiás; Veideiros, Goiás; Bôa Nova, Baía; Cajazeiras, Baía; Aragarcas, Goiás; Brasília, Distrito Federal; Janaúba, Minas Gerais; Belmonte, Baía; Goiânia, Goiás (Trindade); Caldas Novas, Goiás; Rio Verde, Goiás; Rio São Francisco, Minas Gerais; Miranda, Mato Grosso; Salobra, Mato Grosso; Campo Grande, Mato Grosso; Tres Lagôas, Mato Grosso; Pedregulho, São Paulo; Guarapari, Espírito Santo; Campeiro, Mato Grosso; Glycerio, São Paulo; Rincão, São Paulo; Alfenas, Minas Gerais; Rio Muriaé, Rio de Janeiro; Vaccaria, Mato Grosso; Lins, São Paulo; Descalvado, São Paulo; Bebedouro, São Paulo; Bauru, São Paulo; *Fazenda Barreiro Rico, São Paulo (Anhembí; Victoria; Capivary); Avaré,

São Paulo; San José do Rio Pardo, São Paulo; Ipanema, São Paulo; São Paulo, São Paulo (Emas); Itararé, São Paulo. PARAGUAY, Niu Poná, Yhu. ARGENTINA, Arroyo Urugua-i, Misiones.

MORPHOLOGICAL INTERGRADATION BETWEEN *bahiae* AND *tyrannulus*

The morphological distinction between *bahiae* and *tyrannulus* rests upon the relative extent and distribution of Fuscous and Antique Brown coloration in the tail, but the character is a variable one. Specimens of *tyrannulus* well removed from the range of *bahiae* very rarely exhibit the rectrix pattern of *bahiae* (AMNH 497057, from French Guiana, the type locality of *tyrannulus*; AMNH 497089, from Venezuela; AMNH 97067, from Colombia; and AMNH 320936, from Paraguay). Likewise, within the range of *bahiae* there are occasional specimens that cannot be separated from *tyrannulus* with certainty (AMNH 497147, from São Paulo; AMNH 244140, from Bahia, the type locality of *bahiae*; and AMNH 244166, from Ceará). Cory's "*pallescent*" (1916) was based on two such specimens, taken at one locality in Ceará.

A series of American Museum specimens from Chapada, Mato Grosso, illustrates the entire range of variation in this character in a region where the ranges of the two forms come in contact:

AMNH 33130, typically *bahiae*—maximum amount of Fuscous

AMNH 33110, atypical *bahiae*—diffuse stripe of Fuscous in sixth rectrix; stripe on second rectrix measureable in width

AMNH 33109, difficult to assign to race—Fuscous stripe in sixth rectrix broadens distally only; stripe on second only barely broadened distally, and measureable

AMNH 33128, difficult to assign to race—Fuscous stripe in sixth and second rectrices broad, and diffuse distally

AMNH 33116, atypical *tyrannulus*—stripes on sixth and second rectrices expanded distally, but Fuscous still much reduced.

AMNH 33117, typically *tyrannulus*—minimum amount of Fuscous; stripe only 3 mm. wide on sixth, no diffusion

Similar intergradation in this character of the

rectrices is apparent in northeastern Argentina (AMNH 795879) and in a series from Rio Branco, Brazil (acknowledged by Zimmer, 1938a; AMNH 236851-236856; FMNH 48806), which are perhaps closest to *bahiae* morphologically, but have the molt schedule of the northern population of *M. t. tyrannulus*.

Specimens of intergrades between *tyrannulus* and *bahiae* examined, 11; localities from north to south (see fig. 76): BRAZIL, Frechal, Rio Branco (Rio Surumú; Limão; Rio Cotinga); Serra Grande, Rio Branco; Chapada, Mato Grosso (Cuiabá).

MYIARCHUS MAGNIROSTRIS (GOULD)

This monotypic species is endemic to the Galapagos Islands, where it has been recorded on all the main islands and is nonmigratory. Although it has been placed in a number of other genera, and has even been considered a monotypic genus (*Eribates* Ridgway), it has all the morphological and behavioral characteristics of *Myiarchus* and is most closely related to *M. tyrannulus* among the continental species.

DIAGNOSIS: The only small *Myiarchus* (wing length less than 80 mm.) with inner vanes of rectrices conspicuously marked (at least 3 mm. wide on one or more rectrices) with Antique Brown in adults. In fresh specimens, mandible pales to a light brown basally and color of mouth lining is pale Orange Yellow.

Vocal responses to intruding conspecifics consist of repeated "huit" notes, slowly modulated whistles (vibrato), and rasps that typically do not involve a pronounced deviation from the carrier frequency. Dawn song consists of complex phrases in which rapid "huit" notes reveal a prominent glissando in descending segment of each component; these phrases are sometimes alternated with isolated "huit" notes.

HABITAT (FIG. 85): Occurs in a variety of habitats in the Galapagos, including arid scrubland, transitional zone, and humid zone. Recorded from sea level to mountain tops well above 900 m.

BREEDING AND ANNUAL CYCLE: The older literature contains references that attest to the fact that *magnirostris* is a cavity nester and habitually uses hair and feathers in the lining (Rothschild and Hartert, 1902; Ridgway, 1907; Gifford, 1919). During my two-week visit to the Galapagos in February 1976 I located four nests, all of which were in cavities in arborescent cacti: one in the trunk of *Opuntia echios* (fig. 87), one in the hollow pad of *Opuntia echios* (fig. 85), and two in hollow limbs of *Jasminocereus howellii* (fig. 87). The height aboveground of the entrances of these four cavities ranged from 1.5 to 3 m. Gifford (1919) has reported the use of cavities in citrus and other trees, at heights of up to 6 m. He also reported use of the globular grass nests of the geospizine finches, lined with the usual hair and feathers. As sources of hair for the nest lining, in addition to the several species of native rodents (*Oryzomys* spp.), there are domesticated mammals on many of the islands. While hiking in the *Scalesia* woodland on Santa Cruz I was educated as to both the tameness of *magnirostris* and to its proclivity toward the use of hair in its nests. An individual made repeated attempts to gather up strands of my wife's hair, hovering inches from her head before darting in to pull on a strand, or landing on her shoulder briefly before flying upward for another try

TABLE 48
Measurements (in Millimeters) in Samples of *Myiarchus magnirostris*

Sample	N	Range	Mean, S.E.	S.D.	C.V.
Wing Length					
Males	28	69 - 75	72.4 ± 0.32	1.69	2.33
Females	15	67 - 75	69.6 ± 0.56	2.16	3.11
Tail Length					
Males	24	62 - 68	65.5 ± 0.38	1.86	2.85
Females	15	59 - 70	62.5 ± 0.74	2.85	4.56

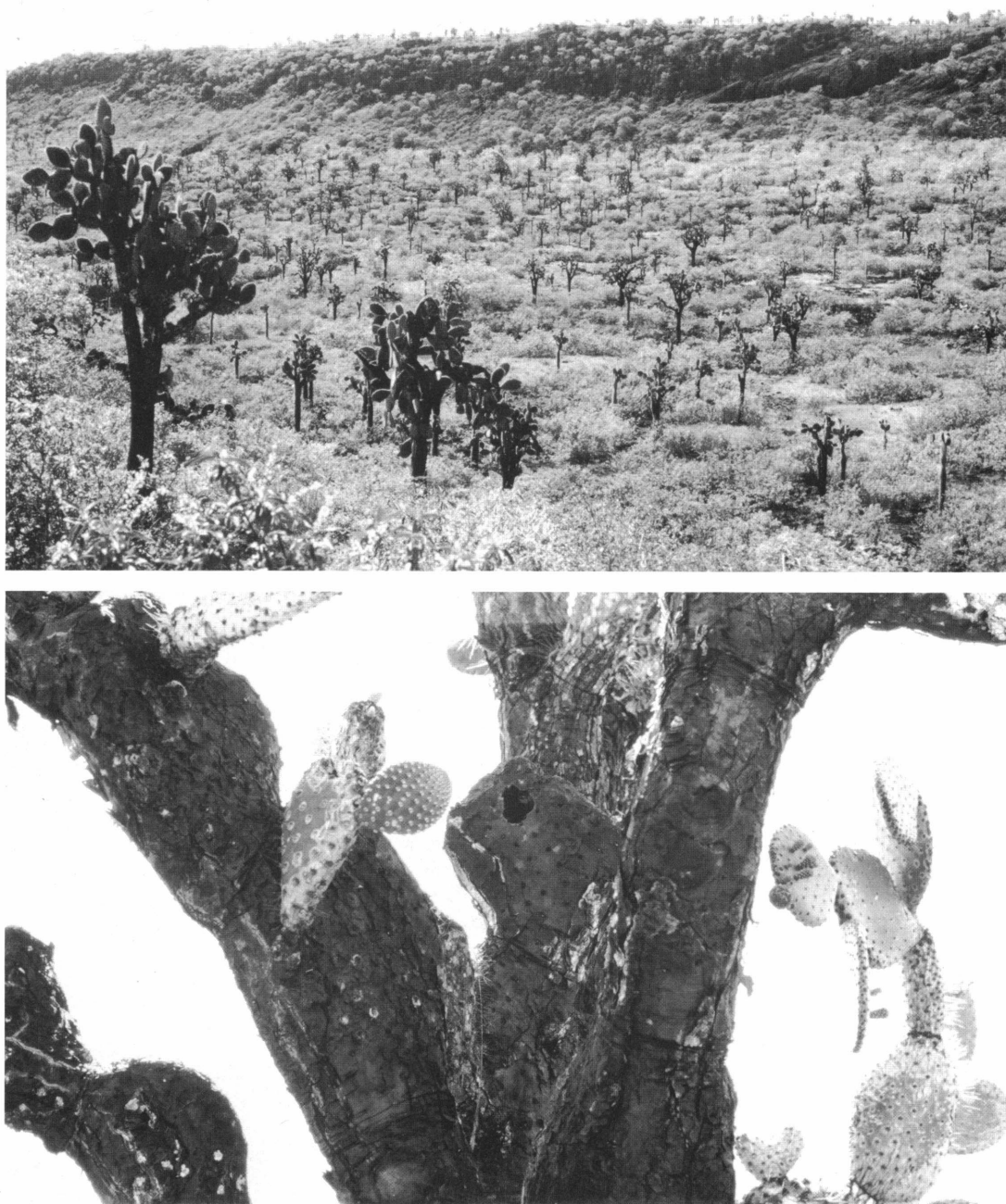


FIG. 85. *Top*: Habitat of *Myiarchus magnirostris* in open woodland (*Opuntia echios*) on Barrington, Galapagos, February 1976; elevation near sea level. *Bottom*: Nest of *M. magnirostris* in hollow pad of an *Opuntia echios*, same locality as above.

(fig. 86). The linings of the two nests I was able to inspect carefully were mostly of fur, feathers, small twigs, and other vegetable matter. Empty cases of insect pupae and unidentified fragments of insects were also included. I could find no pieces of shed reptilian skin. The eggs of *magnirostris* have the ground color and markings characteristic of all continental species of *Myiarchus*.

The breeding season of *magnirostris* appears to be January through March on most of the islands, but the data are insufficient to determine to what degree there is synchrony between islands. On Santa Cruz and Barrington, I found males giving dawn song and females incubating full clutches in mid-February. Two of the four eggs in one of the nests on Santa Cruz hatched during the night or early morning of February 20, my last day on the island.

The complete prebasic molt takes place following breeding, from March through June for most of the island populations. Birds in juvenal plumage have been taken in May and June.

VOCAL CHARACTERS: The analysis of vocal characters of *M. magnirostris* is based on recordings from these samples: Santa Cruz (Indefatigable), seven pairs; Barrington (Santa Fe), two pairs.

CALLS: The vocal repertoire of this species, as determined from the recordings noted above, is summarized in table 1, and illustrated in figures 88 and 89.

In response to playback, or when excited by intruding conspecifics, *M. magnirostris* vocalizes with series of "huit" notes, slowly modulated whistles (vibrato), and rasps. These calls (fig. 88) are similar to their counterparts in the repertoire of the widespread continental relative, *M. tyrannulus*, but average nearly 1 kHz. higher (reflecting the substantially smaller body size of *M. magnirostris*). Rasps are not as conspicuous and consistent in the response of *M. magnirostris* and tend to have less deviation from the carrier frequency, though the modulating frequency appears to be about the same in both species. I do not have daytime recordings of rapid "huit" notes in my samples, though they are a consistent component of the dawn song.

As with *M. tyrannulus*, foraging individuals of *M. magnirostris* not excited by playback or

intruding conspecifics will deliver isolated "huit" notes at irregular intervals, as well as the "whay-burg" call (fig. 88:8-11). In the "whay-burg" note of this species, however, the second part of the call is more likely to be a continuous, slowly modulated vibrato rather than a series of pulsed "huit" notes as in *M. tyrannulus*.

DAWN SONG: The dawn song of the male *M. magnirostris* (fig. 89) consists principally of the repetition of a complex phrase normally derived from the introductory "whay-burg" note and a series of rapid "huit" notes. Only two out of the nine males of *M. magnirostris* samples consistently alternated these complex phrases with isolated "huit" notes, which is the rule for the continental *M. tyrannulus*. The complex phrase tends to be of greater duration than that found in the dawn song of *M. tyrannulus*, and the carrier frequency of the components is nearly 1 kHz. higher than in *M. tyrannulus*. If a slowly modulated vibrato is



FIG. 86. *Myiarchus magnirostris* gathers nesting material (hair from head of author's wife) in *Scalesia* woodland on Santa Cruz, Galapagos, February 1976; elevation 600 m.

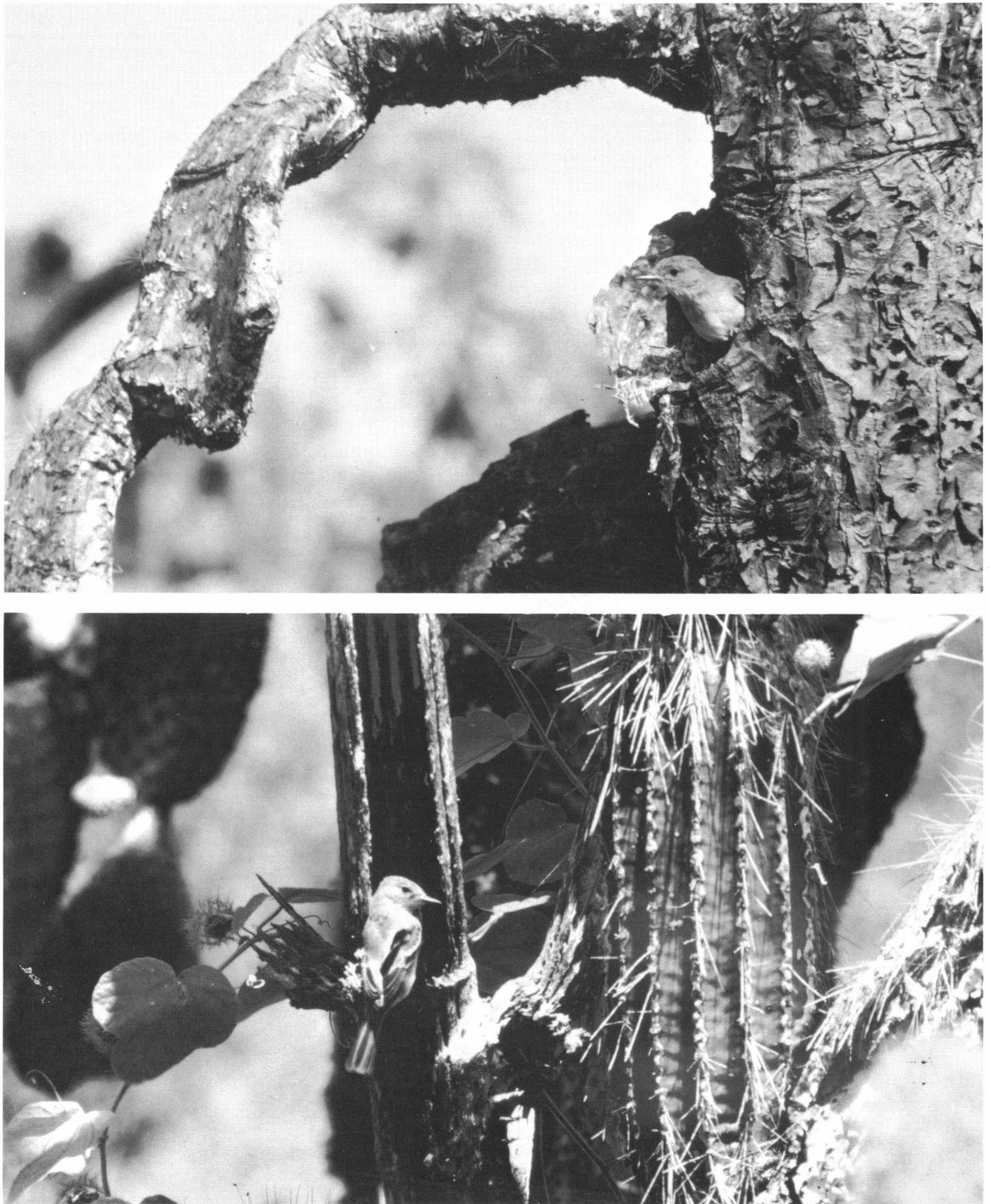


FIG. 87. Nest cavities used by *Myiarchus magnirostris* in the Galapagos. *Top*: In trunk of *Opuntia echios*, near Academy Bay, Santa Cruz, February 1976; elevation 30 m. *Bottom*: In hollow limb of *Jasminocereus howellii*, near Academy Bay, Santa Cruz, February 1976; elevation 25 m. Both photographs taken with a 300 mm. lens, without a blind.

included at all, it generally forms the terminal component of the phrase. It is curious that, in the series of rapid "huit" notes in my sample of dawn song of *M. magnirostris*, the displays show a more prominent glissando in the terminal or descending segment of the "huit" note

rather than in the ascending portion as in *M. tyrannulus*.

GEOGRAPHICAL VARIATION: My samples from Santa Cruz and Barrington islands (about 20 km. apart) do not suggest geographical variation.

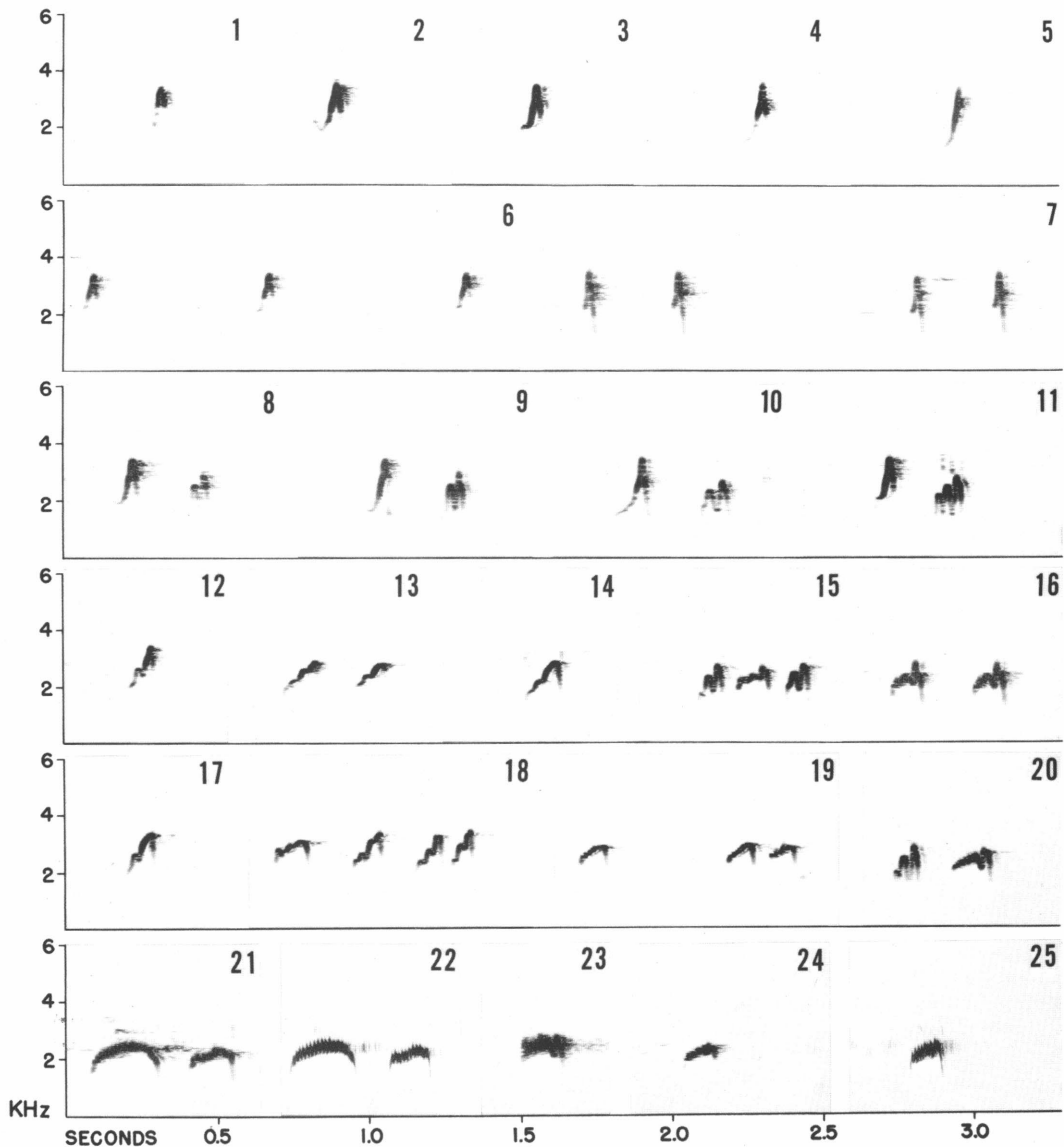


FIG. 88. Variation in vocal characters of *Myiarchus magnirostris*: "huit" notes (1-7), "whay-burg" notes (8-11), slowly modulated whistles (vibrato) (12-20), and rasps (21-25). Spectrograms were made from recordings of birds on Santa Cruz (1-16, 21-25) and on Barrington (17-20) Islands in the Galapagos. The 300 Hz. filter was used for 22 and 25 only.

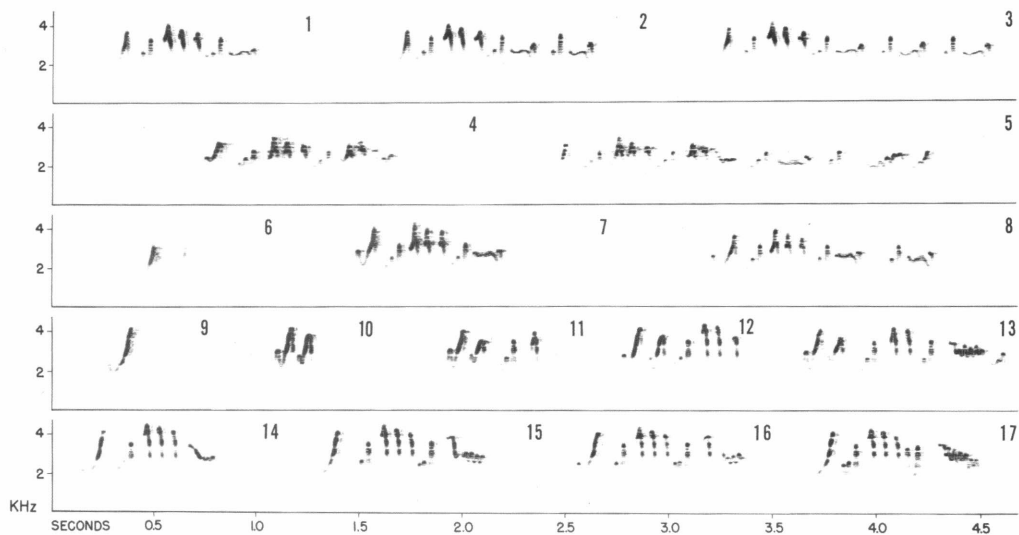


FIG. 89. Variation in vocal characters of *Myiarchus magnirostris*: dawn song. Spectrograms were made with 45 Hz. filter and are from recordings of birds on Santa Cruz (1-8) and on Barrington (9-17) Islands in the Galapagos.

ITINERARY OF FIELDWORK

1976—February 6-20, on the islands of Santa Cruz (Indefatigable) and Barrington (Santa Fe) in the Galapagos.

SYSTEMATICS

Myiarchus magnirostris (Gould)

Tyrannula magnirostris Gould, in Darwin, 1838, pl. 8.

Myiobius magnirostris Gould, in Darwin, 1839, p. 48 (type locality, Chatham Island, Galapagos; holotype in the British Museum [Nat. Hist.]).

Myiarchus magnirostris: Sclater and Salvin, 1870, p. 323 (new combination). Sclater, 1888, p. 262. Berlepsch, 1907, p. 477. Swarth, 1931, p. 84 (synonymy). Zimmer, MS.

Empidonax magnirostris: Baird, Brewer, and Ridgway, 1874, p. 365 (new combination).

Eribates magnirostris: Ridgway, 1893, p. 606 (new combination). Ridgway, 1907, p. 605 (synonymy). Hellmayr, 1927, p. 187 (synonymy).

DISTRIBUTION AND SPECIMENS EXAMINED: Widely occurring on all the main islands in the Galapagos. No other species of *Myiarchus* has been reported from the Galapagos.

Specimens examined, 88; localities include all of the major islands within the Galapagos.

REMARKS: Ridgway (1893) erected a monotypic genus *Eribates* for this species on the basis of its "very long tarsus," and Hellmayr (1927) concurred. I agree with Swarth (1931) and Zimmer (MS) that this is not justified. The relatively long tarsus is presumably a reflection of an insular effect operating during the long period of isolation of *magnirostris* from continental populations. Certainly the foraging behavior, tendency to erect the feathers of the crown when excited, cavity nesting, use of fur and feathers as nest lining, coloration of the eggs, vocalizations, general morphology, and plumage coloration argue for retention of this Galapagos species in *Myiarchus*.

The principal purpose of my visit to the Galapagos was to acquire the kind of data necessary to decide which of the continental species is most closely related to *magnirostris*. I have documented the vocal repertoire of *magnirostris* (p. 605) and indicated its similarity to that of *M. tyrannulus*. The mouth lining of individuals netted on Santa Cruz was a pale yellow, as in *M. tyrannulus*, and the extent of Antique Brown in the tail supports a close relationship with that continental species.

Because of the close similarity in the vocal repertoires of *M. magnirostris* and *M. tyran-*

nulus, I was interested in finding the degree to which territorial pairs of *magnirostris* would respond to the stimulation of my standardized playback tapes of various populations of *M. tyrannulus*. A total of 26 playback experiments was conducted with four territorial pairs of *magnirostris* on the grounds of the Charles Darwin Research Station, Academy Bay, Santa Cruz. None of these birds showed any response to the playback of the following continental or West Indian species: *M. swainsoni*, *M. ferox*, *M. tuberculifer*, *M. cinerascens*, *M. nuttingi*, *M. crinitus*, *M. stolidus*, *M. oberi*, *M. sagrae*, and *M. validus*. The playback tapes of *M. tyrannulus* (Mexico) and *M. tyrannulus* (Argentina), and *M. nugator* (a recent Lesser Antillean derivative of *M. tyrannulus*; see Lanyon, 1967) were the only ones, other than the tape of *magnirostris* itself, to elicit any degree of response in these experiments, and the level of response to these three tapes was extremely low and inconsistent. When given the opportunity, *magnirostris* had no difficulty in discriminating between its own voice and tapes of either *tyrannulus* or *nugator*. The following field notes, made on February 12, 1976, typify the discriminatory ability of these *magnirostris*:

Experiment 20—study area two. Tapes used, *M. magnirostris* vs. *M. tyrannulus* (Mexico). Location of pair unknown at start at 8:25 A.M. One showed at *magnirostris* recorder within one minute. In silent study at 10 ft. from recorder. Several crisscrosses. Both birds near *magnirostris* recorder at 8:28. Crisscrossing within 8 ft. radius at 8:29. Both within 6 ft. of *magnirostris* recorder at switch. One re-

oriented to within 5 ft. of new *magnirostris* within one minute. Both birds in new area by 8:31:30. One calling excitedly at 4 ft. from *magnirostris* recorder. Other at 10 ft. Both in repeated crisscrosses. One dove at recorder, at 8:34, coming to within 1 ft. of it. Repeated crisscrosses by both birds within an 8 ft. radius of the *magnirostris* recorder. Still there, very excited at end of experiment. Good, strong, consistent response to *magnirostris*, including re-orientation. No response to *M. tyrannulus* (Mexico).

Experiment 21—same locality, pair, and date as above. Tapes used, *M. crinitus* vs. *M. validus*. Pair given a five minute rest after previous experiment. Pair calling sporadically in vicinity of *validus* recorder at start at 8:40 A.M. Pair moved out of experimental area at about 8:42, and did not return. Discontinued the experiment at the time of the cable switch, for they showed no interest in either recording. Can see the pair feeding outside the experimental area.

Experiment 22—same locality, pair, and date as above. Tapes used, *M. magnirostris* vs. *M. tyrannulus* (Argentina). Start at 9:05 A.M. Location of pair unknown. Both birds appeared within 30 seconds, in *magnirostris* area. Crisscrossing *magnirostris* recorder within radius of 10 ft., calling well. Pair remained responsive in *magnirostris* area up until time of cable switch, with many crisscrosses, some as close as 1 ft. from recorder. Both birds reoriented to new *magnirostris* recorder within 30 seconds after switch. Both within 6 ft. of new *magnirostris* at 9:11, calling well. Crisscrossing repeatedly, within 10 ft. radius of *magnirostris* recorder. Crisscrossing within 6 ft. radius at 9:14. Remained active and responsive up until end of experiment. No response at all to *M. tyrannulus* (Argentina).

APPENDIX

Data for Sound Recordings Used for the Spectrograms Figured in the Present Report

Figure	Taxon	Locality	Date	Catalogue Number
2: 1	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 12, 1967	125A-099
2: 2	Intergrade between <i>M. s. phaeonotus</i> and <i>M. s. pelzelni</i>	Zanderij, Surinam	Dec. 19, 1970	162B-072
2: 3	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 17, 1974	182A-145
2: 4	<i>M. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 26, 1973	178A-178
2: 5	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-680
2: 6	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-189
2: 7	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	April 28, 1968	130B-090
2: 8	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-185

Figure	Taxon	Locality	Date	Catalogue Number
2: 9	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 29, 1968	131A-023
2:10	<i>M. c. caribbaeus</i>	Cubíro, Lara, Venezuela	May 3, 1974	182B-513
2:11	<i>M. venezuelensis</i>	Upata, Bolívar, Venezuela	May 20, 1968	133A-540
2:12	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 11, 1974	183A-574
2:13	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-552
2:14	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 1, 1976	191A-107
2:15	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 25, 1969	139B-402
3: 1	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-082
3: 2	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. pelzelni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 14, 1967	126B-165
3: 3	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 29, 1968	130B-281
3: 4	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 23, 1976	192A-343
3: 5	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-272
3: 6	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-165
3: 7	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 31, 1973	178B-117
3: 8	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-121
3: 9	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-137
3:10	<i>M. magirostris</i>	Santa Cruz, Galapagos Islands	Feb. 9, 1976	191B-366
3:11	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-180
3:12	<i>M. t. tyrannulus</i>	Tobago, West Indies	May 25, 1968	134A-316
3:13	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137A-084
3:14	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-154
3:15	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 24, 1974	185A-416
3:16	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Ipatinga, Minas Gerais, Brazil	Dec. 12, 1967	126B-115
8: 1	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-451
8: 2	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 13, 1967	125A-318
8: 3	<i>M. t. tuberculifer</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 26, 1974	185A-571
8: 4	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-118
8: 5	<i>M. t. tuberculifer</i>	Tumeremo, Bolívar, Venezuela	May 4, 1970	145A-373
8: 6	<i>M. t. nigriceps</i>	Río Palenque, Pichincha, Ecuador	Jan. 5, 1974	180A-116
8: 7	<i>M. t. atriceps</i>	Chinchao, Huánuco, Peru	Nov. 4, 1972	173A-035
8: 8	<i>M. t. pallidus</i>	Cubíro, Lara, Venezuela	May 4, 1974	183A-096
8: 9	<i>M. t. tuberculifer</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 26, 1974	185A-583
8:10	<i>M. t. atriceps</i>	Entre Ríos, Tarija, Bolivia	Nov. 9, 1974	186A-573
8:11	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-428
8:12	<i>M. t. pallidus</i>	Rancho Grande, Aragua, Venezuela	April 30, 1968	131A-232
8:13	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-428
8:14	<i>M. t. pallidus</i>	Barinas, Barinas, Venezuela	May 13, 1968	133A-256
8:15	<i>M. t. pallidus</i>	Cubíro, Lara, Venezuela	May 4, 1974	183A-095
8:16	<i>M. t. tuberculifer</i>	El Palmar, Bolívar, Venezuela	May 20, 1968	133B-428
8:17	<i>M. t. tuberculifer</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 26, 1974	185B-005
8:18	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 11, 1967	125A-034
8:19	<i>M. t. atriceps</i>	Loja, Loja, Ecuador	Jan. 11, 1974	180B-019
8:20	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 9, 1973	176A-071
8:21	<i>M. t. tuberculifer</i>	Phedra, Surinam	Dec. 20, 1970	162B-493
9: 1	<i>M. t. atriceps</i>	Abra de Porcula, Piura, Peru	Dec. 22, 1973	179A-192
9: 2	<i>M. t. tuberculifer</i>	Phedra, Surinam	Dec. 20, 1970	162B-510

Figure	Taxon	Locality	Date	Catalogue Number
9: 3	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 12, 1967	125A-116
9: 4	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-353
9: 5	<i>M. t. tuberculifer</i>	El Palmar, Bolívar, Venezuela	May 21, 1968	134A-083
9: 6	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 11, 1967	125A-029
9: 7	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 9, 1973	176A-080
9: 8	<i>M. t. pallidus</i>	Barinas, Barinas, Venezuela	May 13, 1968	133A-290
9: 9	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-437
9:10	<i>M. t. tuberculifer</i>	El Palmar, Bolívar, Venezuela	May 21, 1968	134A-065
9:11	<i>M. t. atriceps</i>	Pojo, Cochabamba, Bolivia	Nov. 17, 1974	186B-039
9:12	<i>M. t. tuberculifer</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 26, 1974	185A-584
9:13	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 11, 1967	124A-210
9:14	<i>M. t. tuberculifer</i>	San Ramón, Junín, Peru	Nov. 10, 1972	173A-305
9:15	<i>M. t. pallidus</i>	Rancho Grande, Aragua, Venezuela	April 30, 1968	131A-225
10: 1	<i>M. t. tuberculifer</i>	Villavicencio, Meta, Colombia	May 26, 1970	147A-267
10: 2	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 12, 1967	125A-153
10: 3	<i>M. t. atriceps</i>	Entre Ríos, Tarija, Bolivia	Nov. 9, 1974	186A-445
10: 4	<i>M. t. tuberculifer</i>	Phedra, Surinam	Dec. 20, 1970	162B-543
10: 5	<i>M. t. nigriceps</i>	Río Palenque, Pichincha, Ecuador	Jan. 5, 1974	180A-087
10: 6	<i>M. t. pallidus</i>	Barinas, Barinas, Venezuela	May 13, 1968	133A-231
10: 7	<i>M. t. tuberculifer</i>	San Ramón, Junín, Peru	Nov. 12, 1972	173A-441
10: 8	<i>M. t. atriceps</i>	Loja, Loja, Ecuador	Jan. 8, 1974	180A-285
10: 9	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-452
10:10	<i>M. t. atriceps</i>	Entre Ríos, Tarija, Bolivia	Nov. 9, 1974	186A-379
10:11	<i>M. t. tuberculifer</i>	San Ramón, Junín, Peru	Nov. 12, 1972	173A-431
10:12	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 31, 1973	178B-115
10:13	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-300
10:14	<i>M. t. pallidus</i>	Rancho Grande, Aragua, Venezuela	May 4, 1968	131B-158
10:15	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Dec. 1, 1970	160B-596
11: 1	<i>M. t. tuberculifer</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 26, 1974	185A-580
11: 2	<i>M. t. pallidus</i>	Rancho Grande, Aragua, Venezuela	May 4, 1968	131B-147
11: 3	<i>M. t. brunneiceps</i>	Cerro Azul, Panamá, Panama	April 20, 1969	137A-295
11: 4	<i>M. t. nigriceps</i>	Popayán, Cauca, Colombia	Mar. 31, 1973	178B-140
11: 5	<i>M. t. atriceps</i>	Tucumán, Tucumán, Argentina	Nov. 13, 1967	125A-282
24: 1	<i>M. venezuelensis</i>	Cerro Alto del Cedro, Zulia, Venezuela	May 14, 1970	146A-196
24: 2	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-270
24: 3	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-275
24: 4	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 17, 1968	130A-456
24: 5	<i>M. venezuelensis</i>	Upata, Bolívar, Venezuela	May 6, 1970	145B-179
24: 6	<i>M. venezuelensis</i>	Tobago, West Indies	May 25, 1968	134A-351
24: 7	<i>M. venezuelensis</i>	Tobago, West Indies	May 24, 1968	134A-237
24: 8	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 29, 1968	130B-343
24: 9	<i>M. venezuelensis</i>	Upata, Bolívar, Venezuela	May 6, 1970	145B-139
24:10	<i>M. venezuelensis</i>	Tobago, West Indies	May 26, 1968	134B-131
25: 1	<i>M. venezuelensis</i>	Cerro Alto del Cedro, Zulia, Venezuela	May 14, 1970	146A-219
25: 2	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-268
25: 3	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-280
25: 4	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 27, 1968	130A-502
25: 5	<i>M. venezuelensis</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145A-679
25: 6	<i>M. venezuelensis</i>	Tobago, West Indies	May 24, 1968	134A-180
25: 7	<i>M. venezuelensis</i>	Tobago, West Indies	May 24, 1968	134A-343
25: 8	<i>M. venezuelensis</i>	Tobago, West Indies	May 24, 1968	134A-226
25: 9	<i>M. venezuelensis</i>	Cerro Alto del Cedro, Zulia, Venezuela	May 14, 1970	146A-201

Figure	Taxon	Locality	Date	Catalogue Number
25:10	<i>M. venezuelensis</i>	Ocumare de la Costa, Aragua, Venezuela	April 29, 1968	131A-083
25:11	<i>M. venezuelensis</i>	Cerro Alto del Cedro, Zulia, Venezuela	May 14, 1970	146A-219
25:12	<i>M. venezuelensis</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145B-005
25:13	<i>M. venezuelensis</i>	Tobago, West Indies	May 24, 1968	134A-237
25:14	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-278
25:15	<i>M. venezuelensis</i>	Nirgua, Yaracuy, Venezuela	May 7, 1974	183A-279
25:16	<i>M. venezuelensis</i>	Upata, Bolívar, Venezuela	May 20, 1968	133A-490
25:17	<i>M. venezuelensis</i>	Tobago, West Indies	May 25, 1968	134A-545
31: 1	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 7, 1974	186A-140
31: 2	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-085
31: 3	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-184
31: 4	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 3, 1967	123A-024
31: 5	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 4, 1967	126A-366
31: 6	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126B-059
31: 7	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 4, 1967	126A-461
31: 8	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-151
31: 9	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126B-058
31:10	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 12, 1970	161B-588
31:11	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-399
31:12	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-402
31:13	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-279
31:14	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	124B-048
31:15	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. swainsoni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 14, 1967	126B-171
31:16	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 19, 1970	162B-164
31:17	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 19, 1970	162B-056
31:18	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	138A-030
31:19	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	137B-094
31:20	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Las Tres Marías, Corrientes, Argentina	Nov. 16, 1970	156B-358
31:21	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-096
31:22	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	126A-053
31:23	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 12, 1970	162A-010
31:24	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 12, 1970	162A-020
31:25	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126A-589
31:26	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. pelzelni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 13, 1967	126B-132
31:27	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. pelzelni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 12, 1967	126B-087
31:28	<i>M. s. pelzelni</i>	Quillabamba, Cuzco, Peru	Nov. 19, 1972	173B-091
31:29	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-212
31:30	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 21, 1970	163A-108

Figure	Taxon	Locality	Date	Catalogue Number
31:31	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 20, 1970	162B-268
31:32	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 3, 1969	137B-448
31:33	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	138A-079
32: 1	<i>M. s. pelzelni</i>	Quillabamba, Cuzco, Peru	Nov. 19, 1972	173B-126
32: 2	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-234
32: 3	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 19, 1970	162B-083
32: 4	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 20, 1970	162B-268
32: 5	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 1, 1969	137B-067
32: 6	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	138A-055
32: 7	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	138A-080
32: 8	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 3, 1969	137B-448
32: 9	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126B-007
32:10	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-096
32:11	Intergrade between <i>M. s. pelzelni</i> and <i>M. s. phaeonotus</i>	Zanderij, Surinam	Dec. 20, 1970	162B-260
32:12	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 4, 1967	126A-368
32:13	<i>M. s. pelzelni</i>	Quillabamba, Cuzco, Peru	Nov. 19, 1972	173B-105
32:14	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. ferocior</i>	Entre Ríos, Argentina	Dec. 6, 1970	160A-279
32:15	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-126
32:16	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 3, 1967	123A-089
33: 1	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-087
33: 2	<i>M. s. ferocior</i>	Sáenz Peña, Chaco, Argentina	Nov. 23, 1970	158B-272
33: 3	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 28, 1970	159A-258
33: 4	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123A-531
33: 5	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123A-608
33: 6	<i>M. s. ferocior</i>	Sáenz Peña, Chaco, Argentina	Nov. 23, 1970	158B-270
33: 7	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-093
33: 8	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Las Tres Marías, Corrientes, Argentina	Nov. 19, 1970	157B-322
33: 9	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Las Tres Marías, Corrientes, Argentina	Nov. 19, 1970	157B-302
33:10	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Entre Ríos, Argentina	Dec. 6, 1970	160A-414
34: 1	<i>M. s. phaeonotus</i>	Kavanayén, Bolívar, Venezuela	May 4, 1969	138A-029
34: 2	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-088
34: 3	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-096
34: 4	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126A-597
34: 5	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay	Dec. 7, 1967	126B-050
34: 6	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-080
34: 7	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 4, 1967	126A-463
34: 8	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 10, 1970	161A-085

Figure	Taxon	Locality	Date	Catalogue Number
34: 9	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. pelzelni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 12, 1967	126B-089
34:10	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-352
34:11	<i>M. s. pelzelni</i>	Salvador, Baía, Brazil	Dec. 19, 1967	126B-386
35: 1	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 5-7, 1974	185B-145, 185B-452, 186A-116
35: 2	<i>M. s. ferocior</i>	Villa Montes, Tarija, Bolivia	Nov. 6-7, 1974	185B-452, 186A-116
35: 3	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 29, 1970 Nov. 15, 18, 1967	159A-501 125A-529, 125B-316
35: 4	<i>M. s. ferocior</i>	Tucumán, Tucumán, Argentina	Nov. 15, 1967 Nov. 28, 1970	125A-529 159A-015
35: 5	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Las Tres Marías, Corrientes, Argentina	Nov. 14-17, 1970	156A-437, 158A-039, 157B-111, 156A-465
35: 6	Intergrade between <i>M. s. ferocior</i> and <i>M. s. swainsoni</i>	Las Tres Marías, Corrientes, Argentina	Nov. 18, 14, 1970	158A-201, 156A-465
35: 7	<i>M. s. swainsoni</i>	Anhembi, São Paulo, Brazil	Dec. 12, 1970 Nov. 30, 1967 Dec. 4, 1967	161B-441 126A-136 126A-387
35: 8	<i>M. s. swainsoni</i>	Sierra de Animas, Maldonado, Uruguay Anhembi, São Paulo, Brazil	Dec. 7, 1967 Dec. 4, 1967 Dec. 12, 1970	126A-560 126A-387 162A-100
35: 9	Intergrade between <i>M. s. swainsoni</i> and <i>M. s. pelzelni</i>	Ipatinga, Minas Gerais, Brazil	Dec. 14, 1967	126B-167, 126B-149
35:10	<i>M. s. pelzelni</i> Intergrade between <i>M. s. pelzelni</i> and <i>M. s. swainsoni</i>	Salvador, Baía, Brazil Ipatinga, Minas Gerais, Brazil	Dec. 19, 1967 Dec. 14, 1967	126B-411 126B-181
44: 1	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 2, 1976	192B-247
44: 2	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 17, 1974	182A-145
44: 3	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 23, 1973	177B-381
44: 4	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 2, 1976	192B-208
44: 5	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 18, 1974	182A-167
44: 6	<i>M. apicalis</i>	Cali, Valle, Colombia	Mar. 22, 1973	177B-330
44: 7	<i>M. apicalis</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178B-024
44: 8	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-352
44: 9	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-614
44:10	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-293
44:11	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-049
45: 1	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 16, 1974	182A-076
45: 2	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 24, 1973	178A-037
45: 3	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 2, 1976	192B-192
45: 4	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 18, 1974	182A-148
45: 5	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 16, 1974	182A-059
45: 6	<i>M. apicalis</i>	Cali, Valle, Colombia	Mar. 22, 1973	177B-313

Figure	Taxon	Locality	Date	Catalogue Number
45: 7	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-569
45: 8	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-591
45: 9	<i>M. apicalis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-065
45:10	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-098
45:11	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-145
45:12	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-048
45:13	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-309
45:14	<i>M. apicalis</i>	Dagua, Valle, Colombia	April 18, 1974	182A-167
45:15	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 2, 1976	192B-212
45:16	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 24, 1973	178A-030
45:17	<i>M. apicalis</i>	Dagua, Valle, Colombia	Mar. 24, 1973	178A-021
45:18	<i>M. apicalis</i>	Cali, Valle, Colombia	Mar. 22, 1973	177B-349
45:19	<i>M. apicalis</i>	Cali, Valle, Colombia	Mar. 22, 1973	177B-308
45:20	<i>M. apicalis</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178B-024
45:21	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-569
45:22	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-579
45:23	<i>M. apicalis</i>	Neiva, Huila, Colombia	Mar. 16, 1973	177A-047
50: 1	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 26, 1976	192A-699
50: 2	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-621
50: 3	<i>M. p. phaeocephalus</i>	Santa Rosa, El Oro, Ecuador	Feb. 4, 1976	191A-433
50: 4	<i>M. p. phaeocephalus</i>	Santa Rosa, El Oro, Ecuador	Feb. 4, 1976	191A-430
50: 5	<i>M. p. phaeocephalus</i>	Arenillas, El Oro, Ecuador	Feb. 3, 1976	191A-386
50: 6	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Jan. 31, 1976	191A-038
50: 7	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 1, 1976	191A-102
50: 8	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-296
50: 9	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-268
50:10	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-247
50:11	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-276
50:12	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-231
50:13	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-506
50:14	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-568
50:15	<i>M. p. phaeocephalus</i>	Santa Rosa, El Oro, Ecuador	Feb. 4, 1976	191A-433
50:16	<i>M. p. phaeocephalus</i>	Arenillas, El Oro, Ecuador	Feb. 3, 1976	191A-386
50:17	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 1, 1976	191A-107
50:18	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-261
50:19	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-281
50:20	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-224
50:21	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-224
50:22	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 1, 1976	191A-107
50:23	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-244
50:24	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-244
50:25	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-176
50:26	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 26, 1976	192A-704
50:27	<i>M. p. phaeocephalus</i>	Santa Rosa, El Oro, Ecuador	Feb. 4, 1976	191A-407
50:28	<i>M. p. phaeocephalus</i>	Santa Rosa, El Oro, Ecuador	Feb. 4, 1976	191A-397
51: 1	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 2, 1976	191A-332
51: 2	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 5, 1976	191A-950
51: 3	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 1, 1976	191A-220
51: 4	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-515
51: 5	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 27, 1976	192B-166
51: 6	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-257
51: 7	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-083

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51: 8	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-495
52: 1	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 23, 1976	192A-241
52: 2	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 23, 1976	192A-361
52: 3	<i>M. p. phaeocephalus</i>	Huaquillas, El Oro, Ecuador	Feb. 23, 1976	192A-253
52: 4	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 27, 1976	192B-012
52: 5	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 27, 1976	192B-026
52: 6	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-389
52: 7	<i>M. p. phaeocephalus</i>	Manta, Manabí, Ecuador	Feb. 25, 1976	192A-428
52: 8	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 27, 1973	175A-050
52: 9	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 27, 1973	175A-170
52:10	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 27, 1973	175A-177
52:11	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-171
52:12	<i>M. p. phaeocephalus</i>	Chilaco, Piura, Peru	Feb. 26, 1973	174A-218
55: 1	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-526
55: 2	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-201
55: 3	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-168
55: 4	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-242
55: 5	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-278
55: 6	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-179
55: 7	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-020
55: 8	<i>M. c. cephalotes</i>	San Ramón, Junín, Peru	Nov. 11, 1972	173A-382
55: 9	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	April, 19, 1974	182A-218
55:10	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-251
56: 1	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	April 19, 1974	182A-227
56: 2	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-354
56: 3	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-231
56: 4	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-348
56: 5	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 13, 1973	176B-216
56: 6	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 13, 1973	176B-358
56: 7	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-186
56: 8	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-186
56: 9	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-193
56:10	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-178
56:11	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-178
56:12	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-222
56:13	<i>M. c. caribbaeus</i>	Cubíro, Lara, Venezuela	May 3, 1974	182B-369
56:14	<i>M. c. caribbaeus</i>	Cubíro, Lara, Venezuela	May 3, 1974	182B-369
56:15	<i>M. c. caribbaeus</i>	Cubíro, Lara, Venezuela	May 3, 1974	182B-504
56:16	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-360
56:17	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 10, 1973	176A-360
56:18	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 11, 1974	183A-622
56:19	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-018
56:20	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-345
56:21	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-333
57: 1	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-015
57: 2	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-002
57: 3	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-046
57: 4	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-026
57: 5	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	April 30, 1974	182B-109
57: 6	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 10, 1974	183A-368
57: 7	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 11, 1974	183B-008

Figure	Taxon	Locality	Date	Catalogue Number
57: 8	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 11, 1974	183A-445
57: 9	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 9, 1974	183A-302
57:10	<i>M. c. cephalotes</i>	San Ramón, Junín, Peru	Nov. 11, 1972	173A-382
57:11	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	May 11, 1974	183B-013
57:12	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	April 19, 1974	182A-233
57:13	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-296
57:14	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-343
57:15	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-354
57:16	<i>M. c. caribbaeus</i>	Colonia Tovar, Aragua, Venezuela	May 6, 1968	132A-347
57:17	<i>M. c. caribbaeus</i>	Cubíro, Lara, Venezuela	May 3, 1974	182B-498
57:18	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-371
57:19	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-343
57:20	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-343
57:21	<i>M. c. cephalotes</i>	Popayán, Cauca, Colombia	Mar. 30, 1973	178A-343
60: 1	<i>M. p. actiosus</i>	Puntarenas, Puntarenas, Costa Rica	Mar. 8, 1976	192B-304
60: 2	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 27, 1973	178A-209
60: 3	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 27, 1973	178A-291
60: 4	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-120
60: 5	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 17, 1973	177A-682
60: 6	<i>M. p. panamensis</i>	Carrasquero, Zulia, Venezuela	May 15, 1970	146A-303
60: 7	<i>M. p. panamensis</i>	Carrasquero, Zulia, Venezuela	May 15, 1970	146A-305
60: 8	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137A-090
60: 9	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 17, 1973	177A-593
60:10	<i>M. p. actiosus</i>	Puntarenas, Puntarenas, Costa Rica	Mar. 9, 1976	192B-392
60:11	<i>M. p. actiosus</i>	Puntarenas, Puntarenas, Costa Rica	Mar. 9, 1976	192B-392
60:12	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 20, 1969	137B-017
60:13	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 20, 1969	137B-017
60:14	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 23, 1973	177B-503
60:15	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 23, 1973	177B-503
60:16	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-552
60:17	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 15, 1973	176B-552
60:18	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 17, 1973	177A-702
60:19	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 17, 1973	177A-702
60:20	<i>M. p. panamensis</i>	Santa Bárbara, Zulia, Venezuela	May 20, 1970	146A-392
61: 1	<i>M. p. actiosus</i>	Puntarenas, Puntarenas, Costa Rica	Mar. 9, 1976	192B-334
61: 2	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137A-084
61: 3	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137B-098
61: 4	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 20, 1969	137B-017
61: 5	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137A-123
61: 6	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-133
61: 7	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-155
61: 8	<i>M. p. panamensis</i>	Carrasquero, Zulia, Venezuela	May 16, 1970	146A-356
61: 9	<i>M. p. actiosus</i>	Puntarenas, Puntarenas, Costa Rica	Mar. 9, 1976	192B-359
61:10	<i>M. p. panamensis</i>	La Jagua, Panamá, Panama	April 19, 1969	137B-017
61:11	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 27, 1973	178A-264
61:12	<i>M. p. panamensis</i>	Buenaventura, Valle, Colombia	Mar. 23, 1973	177B-475
61:13	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	April 22, 1974	184A-044
61:14	<i>M. p. panamensis</i>	Neiva, Huila, Colombia	Mar. 17, 1973	177A-587
66: 1	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 21, 1970	163A-073
66: 2	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 21, 1970	163A-078
66: 3	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 5, 1972	173A-063

Figure	Taxon	Locality	Date	Catalogue Number
66: 4	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 6, 1972	173A-207
66: 5	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Villavicencio, Meta, Colombia	May 25, 1970	146B-212
66: 6	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145A-493
66: 7	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145A-561
66: 8	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	La Morrocuya, Monagas, Venezuela	May 8, 1970	145B-429
66: 9	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 21, 1974	185A-097
66:10	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 21, 1974	185A-077
66:11	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Ipatinga, Minas Gerais, Brazil	Dec. 12, 1967	126B-092
66:12	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 20, 1970	158B-040
66:13	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-184
66:14	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-198
66:15	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-405
66:16	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 5, 1972	173A-143
66:17	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 18, 1970	162B-025
66:18	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	La Morrocuya, Monagas, Venezuela	May 8, 1970	145B-306
66:19	<i>M. f. brunnescens</i>	San Fernando de Apure, Apure, Venezuela	May 13, 1969	138B-112
66:20	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 25, 1969	139B-219
66:21	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Villavicencio, Meta, Colombia	May 25, 1970	146B-242
66:22	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Villavicencio, Meta, Colombia	May 25, 1970	146B-567
66:23	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 24, 1974	185A-395
66:24	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-105
66:25	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161B-019
66:26	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 17, 1970	157A-198
66:27	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 21, 1970	163A-063
66:28	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 5, 1972	173A-010
66:29	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 5, 1972	173A-125
66:30	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 24, 1974	185A-423
66:31	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-382

Figure	Taxon	Locality	Date	Catalogue Number
67: 1	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 18, 1970	162B-025
67: 2	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 18, 1970	162B-032
67: 3	<i>M. f. ferox</i>	San Ramón, Junín, Peru	Nov. 13, 1972	173A-531
67: 4	<i>M. f. ferox</i>	San Ramón, Junín, Peru	Nov. 13, 1972	173A-531
67: 5	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145A-431
67: 6	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	El Palmar, Bolívar, Venezuela	May 5, 1970	145A-431
67: 7	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 24, 1969	139B-071
67: 8	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 24, 1974	185A-427
67: 9	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-314
67:10	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 17, 1970	157A-260
67:11	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 21, 1970	162B-663
67:12	<i>M. f. ferox</i>	San Ramón, Junín, Peru	Nov. 13, 1972	173A-531
67:13	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 18, 1970	162B-023
67:14	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	La Morrocuya, Monagas, Venezuela	May 8, 1970	145B-307
67:15	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Villavicencio, Meta, Colombia	May 25, 1970	146B-580
67:16	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 24, 1969	139B-072
67:17	<i>M. f. brunnescens</i>	San Fernando de Apure, Apure, Venezuela	May 13, 1969	138A-582
67:18	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 21, 1974	185A-229
67:19	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-105
67:20	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 17, 1970	157A-374
68: 1	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 6, 1972	173A-240
68: 2	<i>M. f. ferox</i>	Tingo María, Huánuco, Peru	Nov. 6, 1972	173A-240
68: 3	<i>M. f. ferox</i>	San Ramón, Junín, Peru	Nov. 13, 1972	173A-482
68: 4	<i>M. f. ferox</i>	Zanderij, Surinam	Dec. 18, 1970	162B-026
68: 5	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Guasipati, Bolívar, Venezuela	May 3, 1970	145A-122
68: 6	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Guasipati, Bolívar, Venezuela	May 3, 1970	145A-122
68: 7	Intergrade between <i>M. f. ferox</i> and <i>M. f. brunnescens</i>	Villavicencio, Meta, Colombia	May 25, 1970	146B-226
68: 8	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 24, 1969	139B-005
68: 9	<i>M. f. brunnescens</i>	San Fernando de Apure, Apure, Venezuela	May 13, 1969	138B-011
69: 1	<i>M. f. brunnescens</i>	Santo Domingo, Táchira, Venezuela	May 25, 1969	139B-403
69: 2	Intergrade between <i>M. f. ferox</i> and <i>M. f. australis</i>	Villa Tunari, Cochabamba, Bolivia	Oct. 21, 1974	185A-164
69: 3	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 15, 1970	156B-002

Figure	Taxon	Locality	Date	Catalogue Number
69: 4	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 15, 1970	156B-002
69: 5	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 15, 1970	156B-025
69: 6	<i>M. f. australis</i>	Las Tres Marías, Corrientes, Argentina	Nov. 15, 1970	156B-025
69: 7	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-430
69: 8	<i>M. f. australis</i>	Anhembi, São Paulo, Brazil	Dec. 11, 1970	161A-430
74: 1	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-140
74: 2	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-140
74: 3	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-137
74: 4	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-138
74: 5	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-136
74: 6	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 29, 1973	179B-139
74: 7	<i>M. semirufus</i>	Casma, Ancash, Peru	Mar. 3, 1973	174B-011
74: 8	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 20, 1973	179A-117
74: 9	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 20, 1973	179A-133
74:10	<i>M. semirufus</i>	Casma, Ancash, Peru	Mar. 3, 1973	174B-038
74:11	<i>M. semirufus</i>	Casma, Ancash, Peru	Mar. 3, 1973	174B-040
74:12	<i>M. semirufus</i>	Casma, Ancash, Peru	Mar. 3, 1973	174B-049
74:13	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-011
74:14	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-014
74:15	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-014
74:16	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-305
74:17	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-305
74:18	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-548
74:19	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-548
74:20	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-030
74:21	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-114
74:22	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-114
75: 1	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-055
75: 2	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179A-518
75: 3	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-516
75: 4	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 25, 1973	179A-514
75: 5	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-101
75: 6	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-077
75: 7	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-123
75: 8	<i>M. semirufus</i>	Casma, Ancash, Peru	Dec. 28, 1973	179B-124
81: 1	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-218
81: 2	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-238
81: 3	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	125B-455
81: 4	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	125B-456
81: 5	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 22, 1968	130A-100
81: 6	<i>M. t. tyrannulus</i>	Barinas, Barinas, Venezuela	May 13, 1968	133A-097
81: 7	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 20, 1968	133B-009
81: 8	<i>M. t. tyrannulus</i>	Tobago, West Indies	May 25, 1968	134B-033
81: 9	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-258
81:10	<i>M. t. tyrannulus</i>	Guasipati, Bolívar, Venezuela	May 2, 1970	145A-091
81:11	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	April 28, 1968	130B-050
81:12	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-205
81:13	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-374
81:14	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 17, 1967	125B-080
81:15	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Dec. 21, 1967	124B-170
81:16	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	126A-001

Figure	Taxon	Locality	Date	Catalogue Number
82: 1	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-251
82: 2	<i>M. t. tyrannulus</i>	Trinidad, West Indies	Mar. 11, 1963	089A-041
82: 3	<i>M. t. tyrannulus</i>	Barinas, Barinas, Venezuela	May 12, 1968	133A-000
82: 4	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	May 1, 1968	131A-331
82: 5	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	April 28, 1968	130B-106
82: 6	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 20, 1968	133B-017
82: 7	<i>M. t. tyrannulus</i>	Guasipati, Bolívar, Venezuela	May 2, 1970	145A-095
82: 8	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 19, 1967	125B-380
82: 9	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 19, 1967	125B-389
82:10	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 4, 1967	123B-257
82:11	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 17, 1967	125B-077
82:12	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-202
82:13	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	125B-513
82:14	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 22, 1968	130A-025
82:15	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-246
82:16	<i>M. t. tyrannulus</i>	Tobago, West Indies	May 25, 1968	134A-308
82:17	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 20, 1968	133B-186
82:18	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 2, 1970	145A-093
82:19	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	April 28, 1968	130B-145
82:20	<i>M. t. tyrannulus</i>	Ocumare de la Costa, Aragua, Venezuela	May 1, 1968	131A-327
82:21	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 20, 1968	133B-159
82:22	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-198
82:23	<i>M. t. tyrannulus</i>	Las Tres Marías, Corrientes, Argentina	Nov. 14, 1970	156A-481
82:24	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 19, 1967	125B-388
82:25	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-445
82:26	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-209
82:27	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 29, 1967	125B-498
82:28	<i>M. t. bahiae</i>	Salvador, Baía, Brazil	Dec. 20, 1967	124B-136
83: 1	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 22, 1968	130A-065
83: 2	<i>M. t. tyrannulus</i>	Barinas, Barinas, Venezuela	May 12, 1968	133A-008
83: 3	<i>M. t. tyrannulus</i>	Pie de Cuesta, Lara, Venezuela	May 3, 1974	182B-553
83: 4	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-282
83: 5	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 5, 1974	185B-218
83: 6	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-245
83: 7	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Dec. 20, 1967	124B-128
83: 8	<i>M. t. bahiae</i>	Salvador, Baía, Brazil	Dec. 21, 1967	124B-185
83: 9	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-253
83:10	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-245
83:11	<i>M. t. tyrannulus</i>	Barinas, Barinas, Venezuela	May 12, 1968	133A-018
83:12	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 2, 1970	145A-090
83:13	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 19, 1967	125B-405
83:14	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-249
83:15	<i>M. t. bahiae</i>	Anhembi, São Paulo, Brazil	Nov. 30, 1967	126A-218
83:16	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 22, 1968	130A-078
83:17	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 20, 1968	133B-013
83:18	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 7, 1967	123B-281
83:19	<i>M. t. bahiae</i>	Salvador, Baía, Brazil	Dec. 20, 1967	124B-076
84: 1	<i>M. t. tyrannulus</i>	Curaçao, Netherlands Antilles	April 23, 1968	130A-128, 130A-156
84: 2	<i>M. t. tyrannulus</i>	Tobago, West Indies	May 25, 1968	134A-313, 134A-316

Figure	Taxon	Locality	Date	Catalogue Number
84: 3	<i>M. t. tyrannulus</i>	Upata, Bolívar, Venezuela	May 4, 1970 May 2, 1970	145A-203 145A-055, 145A-053
84: 4	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 6, 1974	185A-489, 533, 483
84: 5	<i>M. t. tyrannulus</i>	Villa Montes, Tarija, Bolivia	Nov. 6, 1974	186A-073, 185B-530, 185B-478
84: 6	<i>M. t. tyrannulus</i>	Tucumán, Tucumán, Argentina	Nov. 17, 1967	125B-018
84: 7	<i>M. t. tyrannulus</i>	Las Tres Marías, Corrientes, Argentina	Nov. 18, 1970	158A-172
88: 1	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-008
88: 2	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-133
88: 3	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-157
88: 4	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-211
88: 5	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-309
88: 6	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-137
88: 7	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-191
88: 8	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-140
88: 9	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-154
88:10	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-202
88:11	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-155
88:12	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 17, 1976	192A-001
88:13	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-178
88:14	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-327
88:15	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-305
88:16	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-312
88:17	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-546
88:18	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-545
88:19	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-546
88:20	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-538
88:21	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-179
88:22	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-179
88:23	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-186
88:24	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-304
88:25	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 8, 1976	191B-304
89: 1	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 9, 1976	191B-390
89: 2	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 9, 1976	191B-381
89: 3	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 9, 1976	191B-398
89: 4	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-099
89: 5	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-077
89: 6	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-057
89: 7	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 7, 1976	191B-121
89: 8	<i>M. magnirostris</i>	Santa Cruz, Galapagos Islands	Feb. 9, 1976	191B-434
89: 9	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-461
89:10	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-488
89:11	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-480
89:12	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-503
89:13	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-472
89:14	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-507
89:15	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-485
89:16	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-483
89:17	<i>M. magnirostris</i>	Barrington, Galapagos Islands	Feb. 14, 1976	191B-465

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